ISSN 0082-3449

CONTRIBUTIONS IN MARINE SCIENCE

VOLUME 27 SEPTEMBER 1984

CONTRIBUTIONS IN MARINE SCIENCE

VOLUME 27 SEPTEMBER 1984

PUBLISHED BY

MARINE SCIENCE INSTITUTE
THE UNIVERSITY OF TEXAS AT AUSTIN
PORT ARANSAS, TEXAS 78373-1267

FOUNDED BY E. J. LUND IN 1945

Editor: Donald E. Wohlschlag
Editorial Assistant: Ruth Grundy
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VARIABILITY OF WIND-DRIVEN CURRENTS, WEST LOUISIANA INNER CONTINENTAL SHELF: 1978–1979

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ABSTRACT

Two-month summer time series of winds and currents from the west Louisiana inner shelf show little evidence of local wind forcing. Longer records from the fall and winter indicate a strong local current response to the winds associated with cold fronts.

Accepted 9 May 1984

INTRODUCTION

The west Louisiana inner continental shelf slopes gently seaward, creating a wide expanse of shallow water. Much of the substrate is fine-grained material, but occasional sand bodies, *e.g.*, Sabine Bank, rise several meters above the otherwise featureless bottom (Fig. 1).

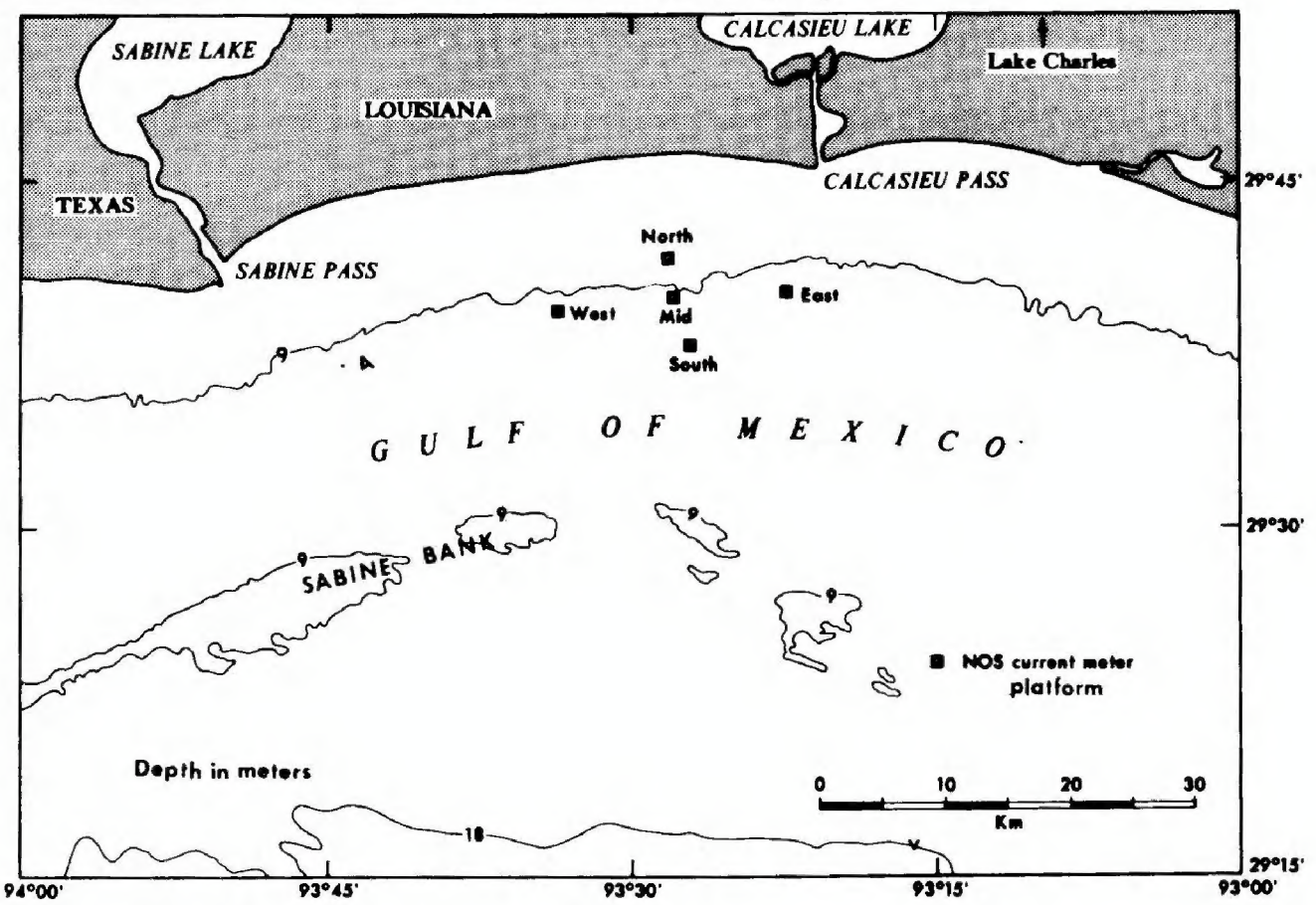

FIG. 1. Chart of the study area.

The current regime over the west Louisiana inner continental shelf varies in response to both seasonal input of fresh water from the Atchafalaya River and seasonal meteorological variability (Kelly, Schmitz, Randall, and Cochrane 1983). Spring flooding of the Atchafalaya River discharges fresh water onto the shelf at an average peak rate of over 11 x 10^3 m^3/s (van Heerden, Wells, and Roberts 1983). The consequent stratification results in a baroclinic coastal boundary layer (Kelly *et al.* 1983). The summer months are characterized by weak southerly and southeasterly winds associated with the dominance of the Bermuda high pressure system. In contrast, the winter season is typified by cold-air outbreaks and strong frontal passages, which recur at intervals of three to ten days.

Current variability in this region is critical to such economically important problems as sediment erosion, transport, and deposition, as well as recruitment of shrimp and menhaden larvae to their nursery grounds. This note represents an analysis of a set of current meter data from the west Louisiana inner continental shelf. It describes the seasonal variability of the subtidal currents and the relation of these currents to the local wind field.

DATA PREPARATION

The study site, located southwest of Calcasieu Pass, Louisiana (Fig. 1), is representative of the west Louisiana inner continental shelf. The bottom is relatively smooth, and local isobaths roughly parallel the coastline. Near-bottom instrumentation was maintained by NOS during the period 1 June 1978 to 1 June 1979 as part of a study for the Strategic Petroleum Reserve Office of the Department of Energy (Frey 1981). Grundy 9021 current meters were fixed on subsurface platforms at 1 and 3 m above the bottom in approximately 9.5 m of water. The platform locations are shown in Fig. 1.

Current velocities were recorded at 5-min intervals during the summer. Data were not recorded during September because of damage by Tropical Storm Debra (Frey 1981). A new sampling rate of 10 min was used when a reduced number of meters were redeployed in October. Furthermore, not all the platforms were instrumented all the time, making it difficult to construct a long time series.

The current at 1-m height is probably within the bottom boundary layer much of the time and is certainly more affected by bottom friction than that at 3 m. The latter should, therefore, provide a better representation of the current throughout the water column. Hydrographic data from the area (Frey 1981) suggest that the water column is often well mixed and a single meter can be assumed to be representative of the entire water column except during late spring and summer, when a vertically stratified baroclinic coastal boundary layer develops. Although autumn and winter alongshelf coherence estimates (not shown) are not as high as expected *a priori*, they are statistically significant at the 95% significance level, and as a result the autumn record from the middle station is merged with the winter record from the west platform to create a continuous time series of current from October through April.

The west Louisiana coastline is aligned nearly east-west; therefore, we chose our alongshelf axis to be aligned east-west. Current components toward the east are referred to as positive v, or alongshelf. Cross-shelf flow components, u, are positive offshore.

A complete year of wind speed and direction at 1-h intervals was available for the period 1 June 1978 to 1 June 1979 from Lake Charles, Louisiana, approximately 55 km northeast of the platforms. Since over-water wind speeds differ from those over land, the Lake Charles wind speeds are transformed to over-water wind speed, U_o, following Hsu (1981),

$$U_o = 3.0\, W^{2/3} \tag{1}$$

where W, the Lake Charles wind speed, and U_o are given in m/sec. The computed wind speeds approximate well to observed over-water winds at our study site when the latter are available for comparison. Total wind stress is then calculated,

$$\tau_w = \rho_a C_D U_o^2 \qquad (2)$$

where ρ_a is air density, 1.2 x 10^{-3}kg/m^3, and C_D is an atmospheric drag coefficient, 1.26 x 10^{-3} (Hsu 1978). Wind stress components are computed using the same coordinate system as for the current. This methodology permits construction of a continuous over-water wind stress record.

In order to investigate low-frequency (<0.5 cpd) fluctuations of wind stress and current, a Lanczos filter with a half-power point of 1.67 days was applied to all of the data and the output resampled at 0.125-day intervals. Variations at diurnal and shorter time scales have been discussed elsewhere (Frey 1981).

The autospectrum of each filtered time series and cross-spectra between series have been computed using a 10-day lag window yielding a frequency resolution of 0.05 cpd and 15 equivalent degrees of freedom. The components of low-passed wind stress and current are divided into six seasonal 60-day periods with a 30-day overlap between the last five periods (see Table 1 for dates and seasonal nomenclature). Table 2 shows mean parameter values for these

TABLE 1

Division of 60-day periods

Summer	2100	7 June	1978	to	2100	6 August	1978
Mid-autumn	2100	8 October	1978	to	2100	7 December	1978
Late autumn	2100	7 November	1978	to	2100	6 January	1979
Early winter	2100	7 December	1978	to	2100	5 February	1979
Mid-winter	2100	6 January	1979	to	2100	7 March	1979
Late winter	2100	5 February	1979	to	2100	6 April	1979

TABLE 2

Mean current speeds and wind stress during the study.

Period *	u (cm/s)	v (cm/s)	τ_x (dyne/cm^2)	τ_y (dyne/cm^2)
Summer	0.6	0.4	-0.2	-0.1
Mid-autumn	-1.0	-7.1	0.0	-0.2
Late autumn	-1.0	-8.8	0.0	-0.3
Early winter	-1.1	-8.2	0.2	-0.2
Mid-winter	-1.2	-4.8	0.2	-0.1
Late winter	-1.1	-5.1	-0.2	-0.2

* See Table 1

six periods. The selection of a 60-day time scale is a compromise designed to give records long enough to contain many realizations of the most energetic events while being short enough to define the seasonal nonstationarity of the processes. The autospectra of the cross-shelf and alongshelf components of wind stress and current are presented in Figure 2 (summer) and Figure 3 (autumn-winter). The filtered time series were not detrended before the spectra were

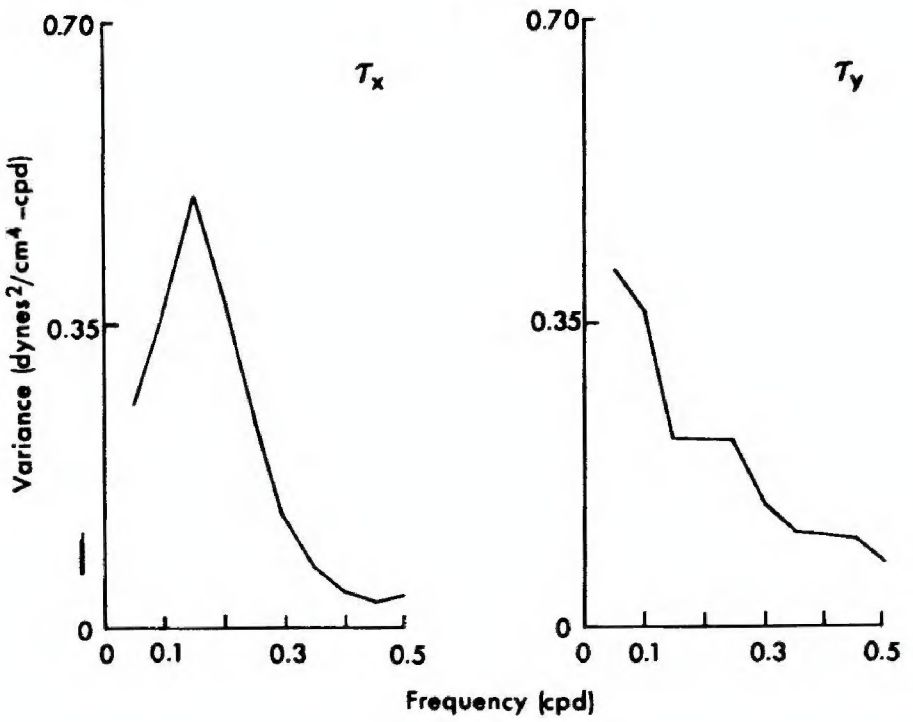

FIG. 2. Spectra of the wind stress and current components during the summer period. Note the change in variance scale for the alongshore current component, *V*.

estimated. The lowest frequency spectral estimate, which contains most of the energy associated with secular trends, was usually lower than the neighboring estimate. Thus a rise in energy at low frequencies may be interpreted as real rather than a reflection of a secular trend.

SEASONAL VARIABILITY

A summer energy density maximum in the cross-shelf wind stress component appears in the 0.15 cpd frequency band. The alongshelf wind stress spectrum, which is approximately equal in amplitude to the cross-shelf stress spectrum, increases monotonically as frequency decreases. Compared to the wind stress variance during the remainder of the year, the

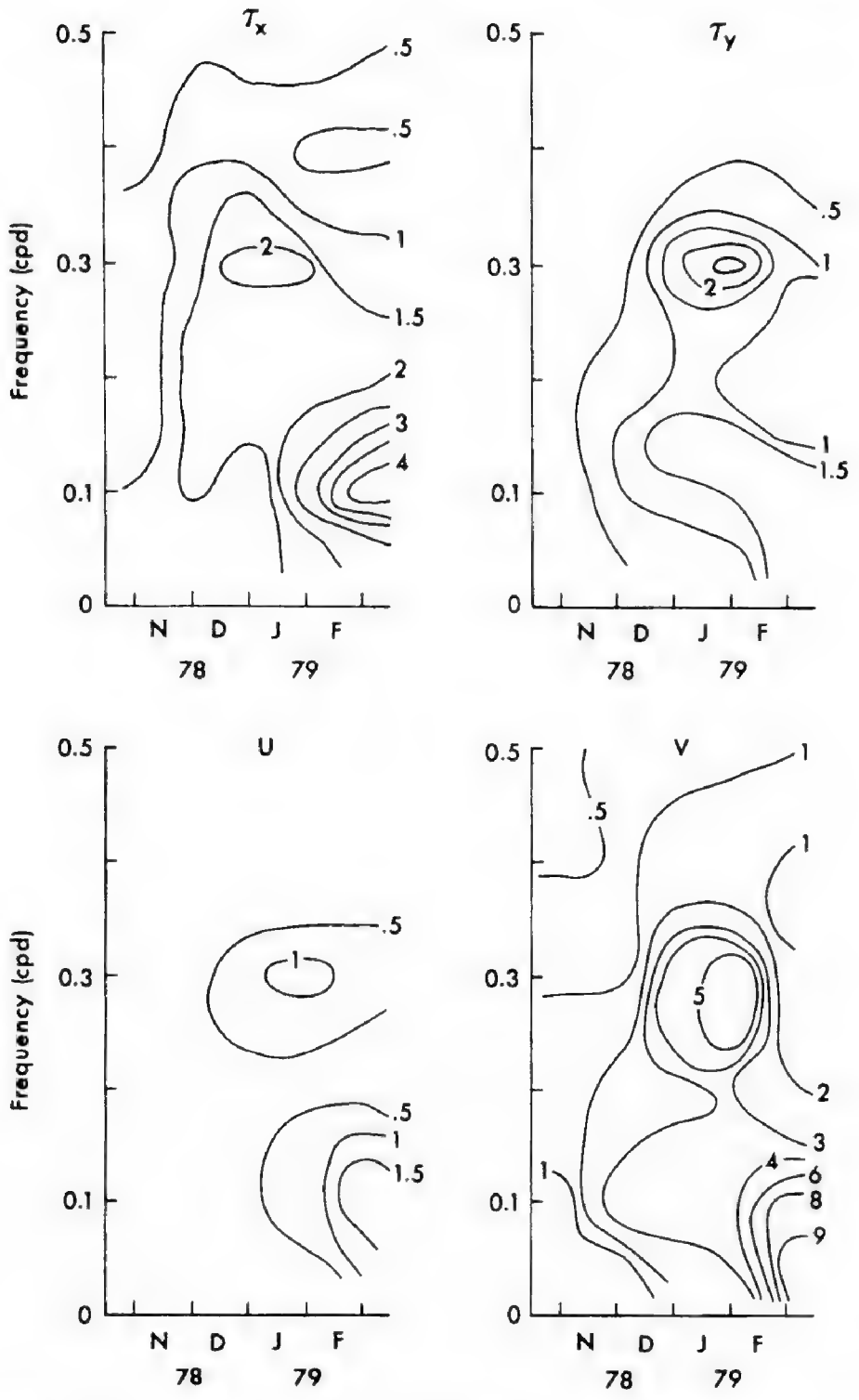

FIG. 3. Contour plots showing the evolution of the spectra of the components of wind stress and current during the fall and winter seasons of 1978–1979. The units of the wind stress spectra are dynes^2/cm^4-cpd. The units of the current spectra are 100 cm^2/s^2-cpd.

summer values are extremely low, resulting from the fact that, other than the infrequent tropical storm or hurricane, the dominant meteorological event in this region during summer is the diurnal sea breeze system, which has been filtered from the data set. The peak in the summer cross-shelf stress spectrum around 0.15 cpd probably reflects weak weather systems, which pass through the region with a recurrence period of 10 to 15 days (DiMego, Bosart, and Endersen 1976).

By mid-autumn there has been a noticeable increase in the wind stress variance (Fig. 3, upper panels). The peak in the alongshelf stress spectrum, while still weak, has shifted to higher frequencies (0.1–0.2 cpd). The most

significant increase occurs in the cross-shelf stress spectrum at the lowest frequencies resolved. Whereas during the summer season the two stress components were equally energetic, the cross-shelf component now dominates. The spectrum amplitudes continue to increase into late autumn.

By early winter, the peak in the cross-shelf stress spectrum has shifted to near 0.3 cpd. Two relative peaks appear in the alongshelf spectrum, one near 0.3 cpd and the other near 0.15 cpd. The peak near 0.3 cpd, which occurs in both spectra, is probably related to frontal passages, which have a recurrence time of 3–10 days (DiMego *et al.* 1976). The 0.3-cpd peak in the alongshelf stress spectrum increases into mid-winter, while in the cross-shelf stress spectrum, a large increase in variance is seen below 0.15 cpd with a peak developing near 0.1 cpd. The most dramatic changes in the late winter season are a decrease in the intensity of the spectrum peak near 0.3 cpd for both components and an increase in variance near 0.1 cpd, particularly in the cross-shelf stress spectrum. The cause of the shift in the frequency of peak stress variance is not clear.

Seasonal variability was also observed in the current velocity autospectra (Fig. 3, bottom panels). During the summer period the spectrum of alongshelf current was of low amplitude and monotonically increasing with decreasing frequency. The cross-shelf spectrum indicates slow, onshore-offshore current variability at 3 meters above the bottom. Indeed, progressive vector diagrams (not shown) exhibit such a pattern. During this period of time, the water column is well stratified and a baroclinic coastal boundary layer occurs in this region (Crout 1982). We believe that the current meter measured flow below the halocline and was isolated from the upper layer, where the wind forcing should be most effective in directly driving an alongshore flow.

The stratification breaks down rapidly during the autumn with the arrival of the first atmospheric cold fronts (Huh, Wiseman, and Rouse 1978). By early autumn, the alongshelf current variance near 0.2 cpd has increased five-fold over its summer value (Fig. 3, lower right). The variance in the alongshelf flow continues to increase into late autumn with a shift in the spectrum peak to frequencies near 0.1 cpd. During the entire autumn period, the variance of the cross-shelf velocity (Fig. 3, lower left) remains small and even decreases at the lowest frequencies. The coastal constraint (Csanady 1981) appears to be significantly affecting the flow.

In early winter, the alongshelf current variance continues to increase, with a principal maximum developing in the spectrum in the 0.25 to 0.3 cpd band (Fig. 3, lower right). A similar but weaker development is seen in the cross-shelf current spectrum (Fig. 3, lower left). A secondary peak in the alongshelf spectrum occurs in the 0.15 to 0.2 cpd band at the same time. As winter progresses, the energy in the alongshelf flow increases; the dominant peak remains at 0.25 to 0.3 cpd (Fig. 3, lower right). The cross-shelf current spectrum (Fig. 3, lower left) at this time displays the same general shape as the alongshore spectrum, but with greatly reduced amplitudes. A dramatic change in the structure of the spectra occurs in late winter. While the total

variance of the alongshelf current increases, the energy in the 0.25 to 0.3 cpd band decreases by over 70% (Fig. 3, lower right). This, though, is compensated by a rapid increase in energy at the lowest frequencies. In a similar fashion, the peak in the cross-shelf spectrum near 0.3 cpd diminishes and a significant peak develops near 0.1 cpd (Fig. 3, lower left). The strength of this latter peak indicates that intense cross-shelf motions are taking place.

The similarity in the autumn-winter wind and current patterns suggests strong wind driving of the coastal currents in the region. It appears that the coastal constraint is directing the flow in the alongshelf direction except in late winter, when the strength of the lowest frequency storms is such as to force significant cross-shelf flow as well. These suggestions will now be examined quantitatively, assuming a linear response, using coherence analysis.

SEASONAL INTERACTIONS

Phase and coherence squared were estimated for the subtidal frequencies in the 60-day seasonal records. The coherence squared values greater than the 95% significance level (0.37) for four time-series pairs are presented in Figure 4 (summer) and Figure 5 (autumn-winter). The two wind stress components are generally incoherent except for a period stretching from later autumn to mid-winter when significant coherence is observed at frequencies less than 0.4 cpd (Fig. 5, upper right).

During the summer period, significant coherence between the currents and the alongshelf stress is found only at the lowest frequencies (Fig. 4, lower panels). In other words, related alongshelf flow can be developed only by winds of frequencies of 0.1 cpd or less. A similar situation occurs east of the Mississippi Delta (Chuang, Schroeder, and Wiseman 1982). The associated phase between alongshelf wind and current at these frequencies implies approximately a 1.5-day lag for the current, which is too long to be attributable to a local frictional effect. The nearshore mean flow at this time of year reverses and runs eastward (Kimsey and Temple 1963, 1964). Our data show an easterly drift from 21 June to 21 July. This reversal appears to be due to a locally wind-driven reversal farther west (Smith 1980). Because the low-frequency meteorological systems are of large scale, it is plausible that the observed coherence is reflective of far-field effects rather than local driving.

In early fall, a peak in the coherence between the alongshelf wind-stress and current is observed in the 0.15 to 0.2 cpd band (Fig. 5, lower right). The water column at this time of year is well mixed, and the currents respond to the wind within half a day. Both these facts point to a change to locally wind-driven dynamics as opposed to summer conditions.

This low-frequency region of high coherence broadens significantly by late autumn, when the peak in the alongshelf stress autospectrum (Fig. 3, upper right) also broadens. The alongshelf current lags the stress by less

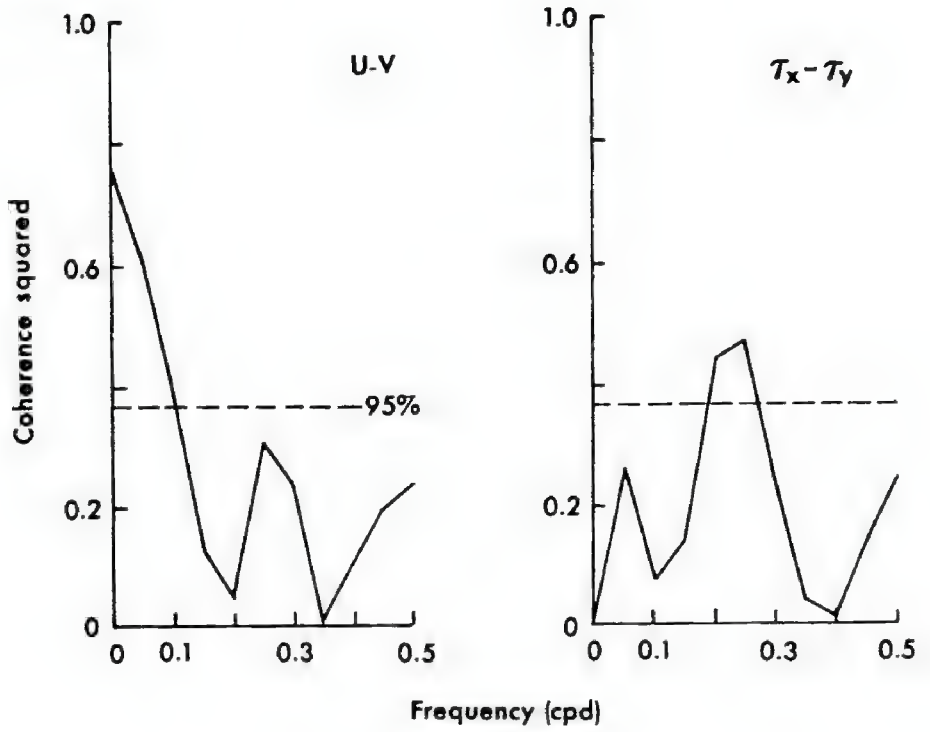

FIG. 4. Coherence squared estimates between the indicated time-series pairs for the summer period. The 95% significance level is shown as a dashed line on each plot.

than 0.5 day at frequencies between 0.1 and 0.25 cpd. The lag is slightly larger within the 0.05 cpd band. The increased energy in the alongshelf currents (Fig. 3, lower right), at these time scales, appears to be a local response to the increased wind stress.

By early winter, the alongshelf stress and current are coherent at all subtidal frequencies (Fig. 5, lower right). Throughout the band from 0.05 to 0.35 cpd, the region where the stress variance is largest, the currents lag the stress by less than 0.5 day. The strongest coherence is associated with the largest wind stress variance, again indicating a local response. The coherence between the two time series is highest in the 0.3 cpd band, but a ridge of high coherence extends toward lower frequencies as the season progres-

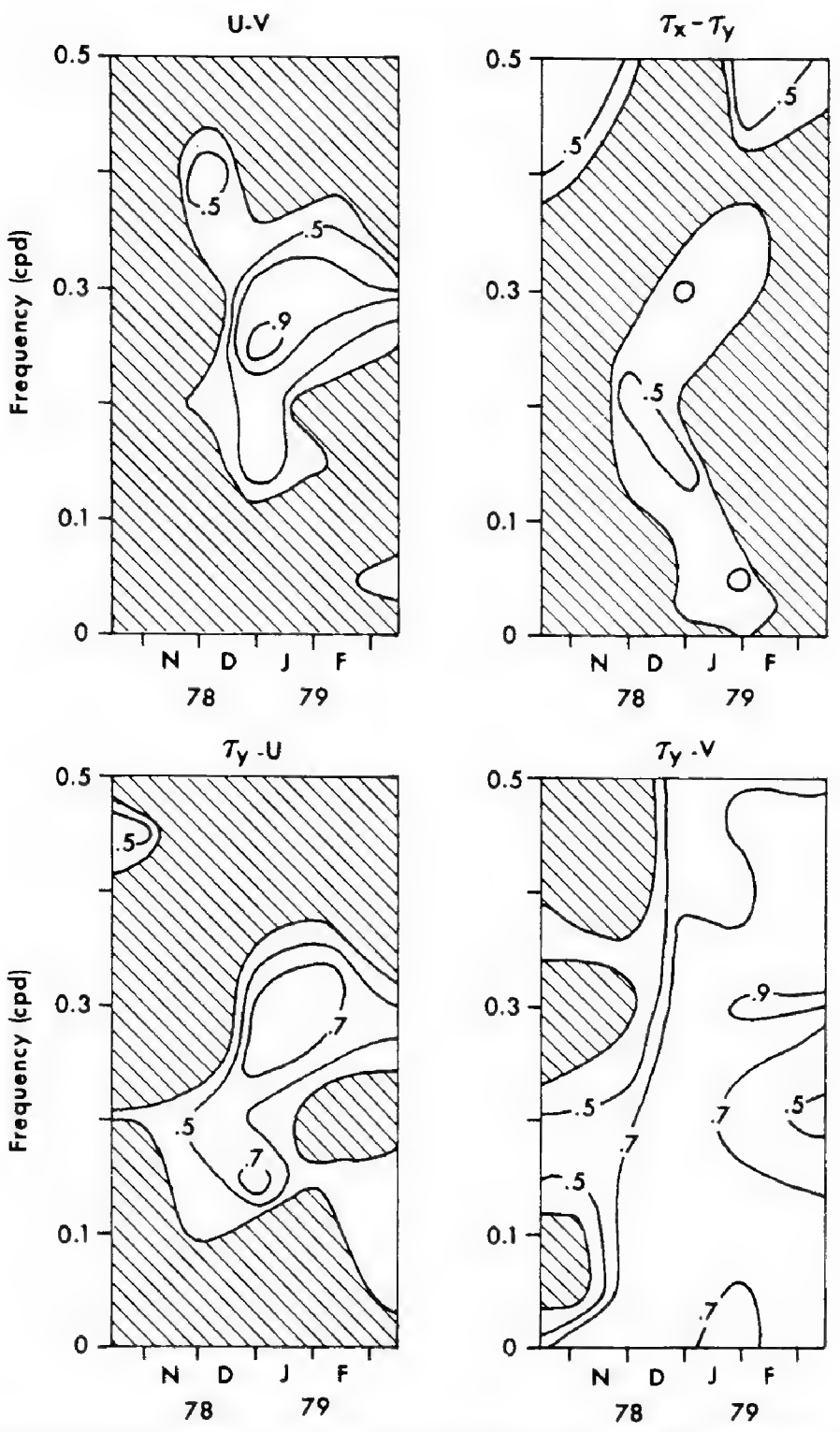

FIG. 5. Contour plots showing the evolution of the coherence squared estimates for the indicated time-series pairs during the fall and winter seasons of 1978–1979. Regions where the estimates fall below the 95% significane level are cross hatched.

ses. The phase again is small. The strong coherence between alongshelf current and stress from late autumn to late winter, particularly near frequencies of 0.3 cpd, supports the hypothesis of a locally wind-driven current forced by atmospheric cold fronts that cross the coastline at an angle. In later winter, the high energy levels of alongshelf current at very low frequencies (Fig. 3, lower right), which are only moderately coherent with the alongshelf stress (Fig. 5, lower right), suggest that a second forcing mechanism may be important in this frequency band. The spring flood of the Atchafalaya River occurs at this time and may well be responsible, through either pressure gradient forcing or inertial effects.

The pattern of coherence between the alongshelf stress and cross-shelf current (Fig. 5, lower left) shows two maxima which are associated with peaks in the alongshelf stress spectrum (Fig. 3, upper right) and similar peaks in the pattern of coherence between the two stress components (Fig. 5, upper right). The phase data show the cross-shelf current to lag the alongshelf stress by nearly 180°.

SUMMARY

The west Louisiana inner continental shelf is subject to intense seasonal variability in stratification and meteorological forcing. This is, in turn, reflected in the subtidal current field. Strong summer stratification results in a well-developed baroclinic coastal boundary layer. Lower layer currents are generally incoherent with the weak summer winds and are probably driven by nonlocal processes.

During autumn, the wind systems become better organized and the associated stress increases, the stratification breaks down, and the subtidal current energy increases. The alongshelf flow appears locally driven by the alongshelf wind stress. This situation persists throughout the winter, although the intensities of both the wind stress and current variability increase and are redistributed in frequency space as the season progresses. Maximum variance occurs at time scales of about 3 days in early and mid winter. In late winter this shifts to scales of 10 days and longer. Late winter is when the Atchafalaya River floods and the alongshelf flow may be strongly influenced by this flood.

ACKNOWLEDGMENTS

This research was supported by a contract with the Coastal Sciences Program, Office of Naval Research, and by the Louisiana Sea Grant College Program, a part of the National Sea Grant College Program, maintained by the National Oceanic and Atmospheric Administration, U.S. Department of Commerce. RLC acknowledges partial support through the Joseph Lipsey, Sr., Memorial Scholarship.

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Contributions in Marine Science. (1984) Vol. 27:13–47.

$\delta^{13}C$ MEASUREMENTS AS INDICATORS OF CARBON FLOW IN MARINE AND FRESHWATER ECOSYSTEMS

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Accepted 19 April 1984

1. INTRODUCTION

Stable isotope ratios provide clues about the origins and transformations of organic matter. A few key reactions control the isotopic composition of most organic matter. Isotopic variations introduced by these reactions are often passed on with little change so that isotopic measurements can indicate natural pathways and flows "downstream" from these key reactions. When chemical and metabolic processes scramble the information content of

molecules, isotopic compositions are often preserved. This realization has prompted increasing use of stable isotope analyses as a tool for understanding complex ecological processes.

Previous reviews have dealt with $^{13}C/^{12}C$ ratios as tracers in geological, plant physiological, and archaeological contexts (Degens 1969, Schwarz 1969, Smith 1972, Kaplan 1975, Deines 1980, van der Merwe 1982, Anderson and Arthur 1983). Brief treatments of isotopic theory are also available (Schowen and Schowen 1981, Hayes 1982). This review deals primarily with stable carbon isotopes, ^{13}C and ^{12}C, as tracers in coastal ecosystems. We focus here on two topics: (1) the origins of sedimentary and suspended organic matter in coastal ecosystems, and (2) the relative importance of various plants as foods for consumers in aquatic food webs. The emphasis of this review is the evaluation of stable isotopes as source indicators (Fig. 1).

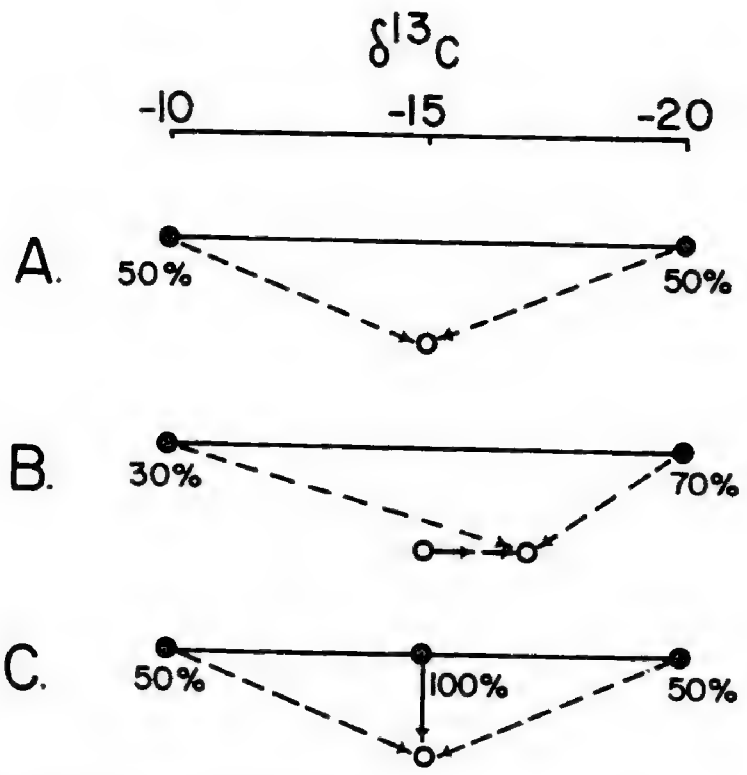

FIG. 1. Interpretation of isotopic mixing models. • = source, o = sample. (a) Two sources separated by 10‰. The sample has an intermediate isotopic value reflecting a simple 50/50 mixture of materials from the two sources. (b) Two-source model, but metabolic processes have changed the isotopic composition of the sample. Correction factors (→) compensating for these changes are applied before calculating the relative contributions of the two sources. (c) Three-source model. The sample may be derived solely from the intermediate source or from a 50/50 combination of the other two sources. Additional information is needed to resolve these alternatives.

In a simple case, two sources that have distinctly different isotopic compositions are present, and isotopic values of samples directly reflect the amounts of the two parent source materials (Fig. 1A). Autotrophic plants and bacteria are considered sources in carbon isotopic mixing models, while samples derived from these sources may be organic matter in sediments, water, or animals (Fig. 1). A refinement of the two-source model corrects for small isotopic changes that occur after mixing has taken place (Fig. 1B). Hetero-

trophic metabolism that occurs in animals, sediments, and water-born organic matter can introduce these relatively small isotopic changes. A final variant of mixing models considers the more complex case where more than two sources are present (Fig. 1C). For this common case in coastal ecology, carbon isotopic values of samples cannot be used unambiguously to indicate sources. Additional information is needed.

Against this background of mixing models, we review several topics in detail: isotopic variability in aquatic primary producers, the marine *vs.* terrestrial origins of organic matter in estuarine sediments, patterns of ^{13}C enrichment in offshore food webs, and isotopic assessments of food webs in salt marshes, seagrass meadows, and lakes and streams. Major conclusions are: (1) the factors controlling stable carbon isotopic compositions of aquatic plants are not completely known, and the isotopic variation observed among aquatic plants is large; (2) consumers at high trophic levels may have isotopic compositions substantially different from those of plants at the base of food webs; (3) macrophytes are less important and benthic algae more important sources of organic matter in estuarine food webs and sediments than once thought; and (4) carbon isotopic measurements are often of limited value in their usefulness for deciphering the complex carbon flows that occur in estuaries. A penultimate section considers supplemental geochemical and isotopic measurements that can aid in the interpretation of $\delta^{13}C$ values.

2. DEFINITIONS AND METHODS

Stable carbon isotope $\delta^{13}C$ values are defined as a parts per thousand or per mil (‰) difference from a standard reference material:

$$\delta^{13}C = \frac{^{13}C/^{12}C_{sample} - {}^{13}C/^{12}C_{standard}}{^{13}C/^{12}C_{standard}} \times 1000$$

The $\delta^{13}C$ definition reflects the method of actual measurement since in the mass spectrometer, CO_2 gases prepared from standard and sample materials are alternately introduced, then compared to obtain an accurate difference measurement. Ratios of the heavy-to-light isotopes are primarily used because day-to-day electronic fluctuations in the mass spectrometer make the measurement of absolute isotopic abundances difficult. Samples enriched in the heavy isotope are "heavier" than other samples and have "higher" or "less negative" $\delta^{13}C$ values. Conversely, samples depleted in the ^{13}C isotope are "lighter" and have "lower" or "more negative" $\delta^{13}C$ values.

The primary standard used in the international literature for reporting $\delta^{13}C$ values is a marine limestone, PDB (Craig 1957). However, the supply of this reference material has been exhausted, and measurements are now made relative to secondary standards—carbonates or organic materials—which have been referenced to the PDB isotopic composition. As the primary standard, PDB has a $\delta^{13}C$ value of 0‰; its $^{13}C/^{12}C$ ratio is 0.0112372 (Craig 1957). Biological materials are usually depleted in ^{13}C relative to PDB and have negative $\delta^{13}C$ values.

Methods of sample preparation vary. For carbon, organic samples can be combusted to CO_2 in a recirculating stream of O_2 (Craig 1953), in an oxygen bomb (Haines and Montague 1979), in a flow-through induction furnace (Parker, Behrens, Calder, and Schultz 1972), in sealed tubes in a muffle furnace (Stump and Frazer 1973; Stuermer, Peters, and Kaplan 1978; Sofer 1980; Boutton, Wong, Hachey, Lee, Cabrera, and Klein 1983), or in an elemental analyzer (J. Hayes

personal communication). Semi-automated commercial units are now available that reduce total sample preparation times (combustion and collection) to five minutes or less for CO_2 (*e.g.*, Isoprep 13, VG Instruments). Combustion must be complete and quantitative, and the use of manganese dioxide and hot metallic copper have been shown to be effective in removing contaminating nitrogen and sulfur gases (Sackett and Thompson 1963, Schwinghamer, Tan, and Gordon 1983). Precision varies with care taken in sample preparation and combustion; well-homogenized samples are particularly important for tissue samples. When necessary, samples are acidified to remove inorganic carbonates ($\delta^{13}C \sim 0‰$) prior to measurement of $\delta^{13}C$ in organic fractions. Typical overall errors for preparation and measurement are $\pm$ 0.1 to $\pm$ 0.3‰.

3. SOURCES OF ORGANIC MATTER IN COASTAL WATERS

3.1. ISOTOPIC VARIATION AND ITS CAUSES IN AQUATIC PLANTS

Aquatic plants show a wide range of isotopic variation. For example, the reported $\delta^{13}C$ range for marine macroalgae is 30‰ (Fig. 2). Large $\delta^{13}C$

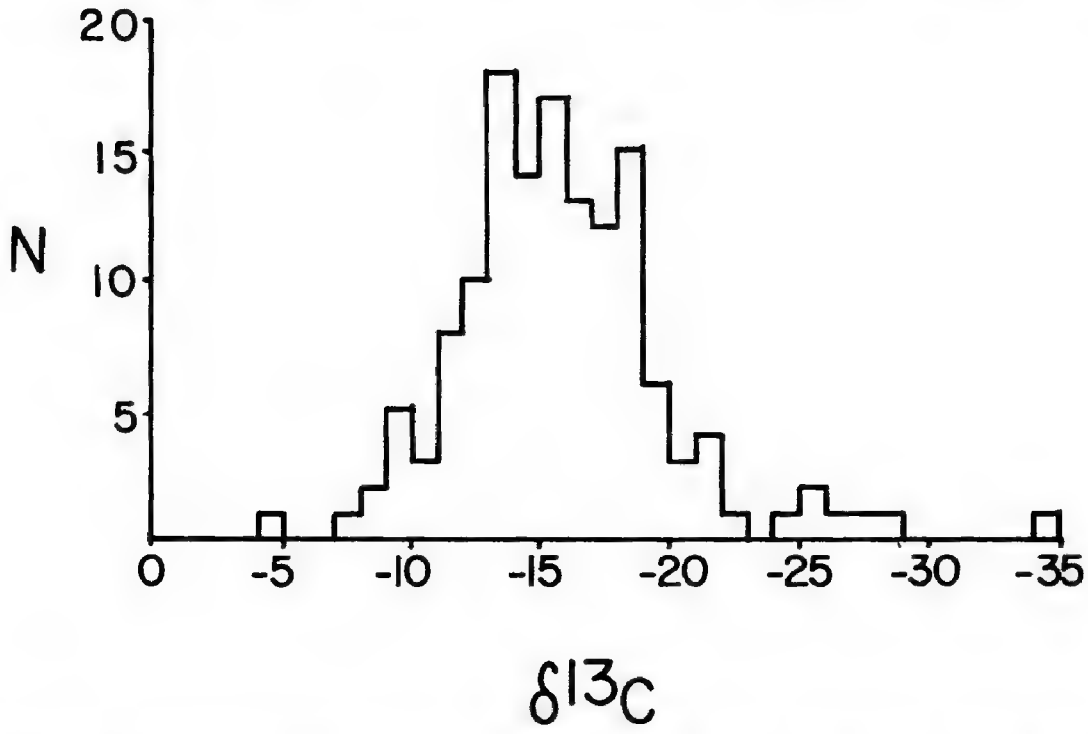

FIG. 2. $\delta^{13}C$ values of benthic marine macroalgae. Sources: Wickman 1952, Craig 1953, Parker 1964, Calder 1969, Calder and Parker 1970, Smith and Epstein 1970, Smith and Epstein 1971, Black and Bender 1976, DeNiro and Epstein 1981b, Fry *et al.* 1982a. Macko *et al.* 1982, Schwinghammer *et al.* 1983, Fry *et al.* 1983b. $\delta^{13}C$ values of plants from Wickman's study were calculated from $^{12}C/^{13}C$ ratios assuming that Wickman's $^{12}C/^{13}C$ ratio of 91 corresponds to $\delta^{13}C = -28.1‰$. This assumption is reasonable since it places Wickman's mean value for terrestrial plants at $\sim -27‰$.

ranges > 10‰ also exist among freshwater plants (Osmond, Valaane, Haslam, Uotila and Roksandic 1981, LaZerte and Szalados 1982) and among seagrass species (McMillan, Parker and Fry 1980). Isotopic variation among individual seagrass blades of the same species at one location can reach 4.7‰ (McMillan *et al.* 1980), and isotopic variations of up to 8‰ have been documented within an individual algal frond (Stephenson, Tan, and Mann 1984).

Farquhar, Ball, von Caemmerer, and Roksandic (1982) have proposed that in aquatic environments, plant $\delta^{13}C$ values are determined by three factors: the isotopic composition of the dissolved inorganic carbon (DIC) pool, the isotopic discrimination of the enzyme responsible for carbon fixation, and the intracellular concentration of CO_2 or HCO_3^- that is the active species fixed by the carboxylating enzyme. The isotopic composition of the dissolved inorganic carbon (DIC) pool can vary; this variation is especially important in low salinity estuarine regions where river water with -5 to -10‰ DIC mixes with ~ 0‰ DIC ocean water (Sackett and Moore 1966, Spiker and Schemel 1979, Sherr 1982, Tan and Strain 1983). DIC with more negative $\delta^{13}C$ values should cause aquatic plants to have more negative $\delta^{13}C$ values since plants obtain their carbon from the DIC pool.

A second factor affecting $\delta^{13}C$ values of aquatic plants is the isotopic discrimination of the carboxylating enzyme responsible for CO_2 fixation. Two enzymes involved in the initial carbon fixation in the C_4 (Hatch-Slack) and C_3 (Calvin) cycles are respectively phosphoenolpyruvate (PEP) carboxylase, and ribulose-1,5-bisphosphate (RuBP) carboxylase. *In vitro* studies have shown that the isotopic discrimination of PEP carboxylase is relatively small at -0.5 to -3.6‰ (Whelan, Sackett, and Benedict 1973, Reibach and Benedict 1977), while that of RuBP carboxylase is much larger, with values usually falling between -23 and -41‰ (Estep, Tabita, Parker, and Van Baalen 1978a, Wong, Benedict, and Kohel 1979, see Estep *et al.* for the complete range of RuBP values). Although variations in aquatic plant $\delta^{13}C$ values are potentially linked to variations in usage of the PEP or RuBP carboxylases, investigations of seagrasses have suggested other explanations. Andrews and Abel (1979) and Benedict, Wong, and Wong (1980) have shown that the seagrasses *Halophila spinulosa, Thalassia hemprichii,* and *T. testudinum* fix CO_2 via Calvin cycle intermediates and should therefore have fairly negative -27‰ values typical of terrestrial C_3 plants. This was not the case, however, as $\delta^{13}C$ values of these seagrasses measured -10 to -14.5‰, which is considerably closer to environmental DIC ($\delta^{13}C \cong 0$‰) than expected for the operation of the RuBP carboxylase (Andrews and Abel 1979, Benedict *et al.* 1980).

Various steps prior to actual CO_2 fixation have been proposed as third factors that exercise the major control on aquatic plant $\delta^{13}C$. Some individual steps which have been suggested as potentially important are diffusion of HCO_3^-/CO_2 across a stagnant boundary layer at the leaf surface, membrane transport of HCO_3^-/CO_2, and dehydration of HCO_3^- to CO_2 inside the cell (Andrews and Abel 1979, Benedict *et al.* 1980, Smith and Walker 1980). If these steps are essentially rate-limiting in the reaction sequence leading to CO_2 fixation, then discrimination at the RuBP carboxylase step will not occur since *all* available CO_2 ($^{13}CO_2$ and $^{12}CO_2$) will be fixed by RuBP carboxylase without isotopic selectivity. Plant $\delta^{13}C$ values will then reflect processes occurring prior to the carboxylation step; these processes typically have smaller (< 10‰) isotopic discriminations associated with them. For example, theoretical calculations suggest that $^{12}CO_2$ diffuses faster than

$^{13}CO_2$ into cell environments by about 4.4‰ (O'Leary and Osmond 1980). If diffusion were very much slower than the subsequent reactions leading to CO_2 fixation, plants should be depleted by only 4.4‰ relative to environmental CO_2. Small depletions of 4–5‰ vs. DIC are in fact observed in some seagrasses and algae (Fry and Parker 1979, DeNiro and Epstein 1981b, Schwinghamer *et al.* 1983), perhaps indicating that diffusion is rate-limiting.

Recent support for the importance of a diffusional barrier comes from studies of freshwater macrophytes (Osmond *et al.* 1981). Whereas diffusion may be important in stagnant waters, in fast-flowing streams the thickness of an unstirred boundary layer next to the leaf surface should be reduced and thereby decrease diffusional resistance to DIC uptake. Larger isotopic discriminations associated with later RuBP carboxylation could then be expressed. These effects may explain the observation that for the pondweed *Potamogeton perfoliatus* L., a small −5‰ isotopic discrimination (plant $\delta^{13}C$ − DIC $\delta^{13}C$) occurs in slow-moving streams while a large −30‰ discrimination occurs in fast-moving streams (Osmond *et al.* 1981).

Other factors that have been shown to influence $\delta^{13}C$ values of autotrophic plants and bacteria include DIC concentration (Abelson and Hoering 1961, Estep 1982), cell density (Pardue, Scalan, Van Baalen, and Parker 1976), and temperature (Degens, Guillard, Sackett and Hellebust 1968b, Wong and Sackett 1978). Much remains to be learned, however. Factors such as the importance of the isotopic exchange reaction between HCO_3^- and CO_2 (Mook, Bommerson, and Staverman 1974), possible isotopic effects accompanying photorespiration, and effects of epiphytes in limiting CO_2 uptake by host plants need to be experimentally assessed before our understanding of aquatic plant $\delta^{13}C$ variations is complete. As a guide for future studies, O'Leary (1981) has published mathematical models for evaluating the probably common and complex situation in which several steps simultaneously influence the rate of CO_2 fixation and plant $\delta^{13}C$.

In summary, the wide $\delta^{13}C$ range among aquatic plants is not understood in detail, although some likely important causes have been identified. Large within-species isotopic variation (> 2‰) occurs on all scales thus far tested, including within individual leaves, among individual leaves, between seasons, and between populations. Great caution should be exercised before assigning average $\delta^{13}C$ values to submerged aquatic plants on the basis of a few measurements.

3.2 $\delta^{13}C$ VALUES OF SOURCE MATERIALS

In spite of the isotopic variation discussed above, marine organic matter in plants, autotrophic bacteria, and peats can often be separated by $\delta^{13}C$ values into fairly distinct groups (Table 1). These divisions into groups are important for constructing mixing models (Fig. 1) and for testing the importance of a specific source by sampling along a gradient towards that source.

TABLE 1

General range of $\delta^{13}C$ values of carbon sources in coastal ecosystems.

Source	$\delta^{13}C$ Usual Range	$\delta^{13}C$ Average Used in Mixing Models
Terrestrial C_3 plants	-23 to -30 [a]	
Terrestrial C_4 plants	-10 to -14 [b]	
River seston (POC)	-25 to -27 [c]	-26
Peat deposits	-12 to -28 [d]	
C_3 marsh plants	-23 to -26 [e]	
C_4 marsh grasses	-12 to -14 [e]	-13
Seagrasses	- 3 to -15 [f]	-10
Macroalgae	- 8 to -27 [g]	
Benthic unicellular algae	-10 to -20 [h]	-17
Temperate marine phytoplankton	-18 to -24 [i]	-21
River-estuarine phytoplankton	-24 to -30 [j]	
Autotrophic sulfur bacteria	-20 to -38 [k]	
Methane-oxidizing bacteria	-62 [l]	

[a] Smith and Epstein 1971.
[b] Deines 1980.
[c] Schultz and Calder 1976, Tan and Strain 1983.
[d] Emery *et al.* 1967, Hunt 1970, Brinson and Matson 1983, Schell 1983.
[e] Haines 1976b, Smith and Epstein 1970.
[f] McMillan *et al.* 1980.
[g] See Figure 1.
[h] Haines and Montague 1979, Incze *et al.* 1982.
[i] Deuser 1970, Haines and Montague 1979, Gearing *et al.* 1984.
[j] Spiker and Schemel 1979, Sherr 1982, Tan and Strain 1983.
[k] Peterson *et al.* 1980, Bondar *et al.* 1976.
[l] Zyakun *et al.* 1981; the range for these bacteria is likely to be large since methane in sediments can have $\delta^{13}C$ values between -20 and -90 o/oo (Schoell 1982) and cell biomass of methane oxidizers measures -12 o/oo *vs.* methane.

3.2.1. Vascular Plants

Intertidal emergent plants such as the C_4 grass *Spartina alterniflora* ($\delta^{13}C$ of $-13‰$, Haines and Montague 1979, Hughes and Sherr 1983) and the C_3 plant *Juncus romerianus* ($\delta^{13}C = -26‰$, Hughes and Sherr 1983) are important sources of organic matter in marshes. Submerged seagrasses are important in some shallow ecosystems. Although the total range in $\delta^{13}C$ values of seagrass species extends from -3.0 to $-23.8‰$ (McMillan *et al.* 1980), most seagrass species show field $\delta^{13}C$ values between -3 and $-15‰$, with an average stable isotope composition of about $-10‰$ for species such as *Thalassia, Zostera,* and *Halodule* (Craig 1953; Parker 1964; Doohan and Newcomb 1976; Benedict and Scott 1976; Fry, Scalan, and Parker 1977; Thayer, Parker, LaCroix, and Fry 1978; McMillan *et al.* 1980; Fry, Lutes, Northam, Parker, and Ogden 1982a). *Syringodium* has the least negative $\delta^{13}C$ values among seagrasses (McMillan *et al.* 1980).

3.2.2. Benthic and Epiphytic Algae

Benthic and epiphytic algae, both macrophytic and microscopic, have a large range of reported $\delta^{13}C$ values that vary from -5 to $-12‰$ for some macrophytes and benthic microalgal mats to $-34.7‰$ for an unidentified red alga (Calder and Parker 1973; Barghoorn, Knoll, Dembicki, and Meinshein 1977; DeNiro and Epstein 1981b; Fry, Scalan, Winters, and Parker 1982a; Incze, Mayer, Sherr, and Macko 1982; Schwinghamer *et al.* 1983; Fry, Scalan and Parker 1983b). More generally, benthic and epiphytic algae have $\delta^{13}C$ values between $-8‰$ and $-27‰$ (Haines and Montague 1979, Thayer *et al.* 1978, Fig. 2).

3.2.3. Phytoplankton and POC

Very few isotopic measurements have been made of phytoplankton. More typically, particulate organic carbon (POC) collected on a filter is measured. This material represents a variable mixture of living and dead phytoplankton, bacteria, and other components. POC is representative of phytoplankton carbon in that it is largely derived from phytoplankton. However, direct $\delta^{13}C$ comparisons of POC and phytoplankton carbon have not been reported so that their isotopic similarity cannot be firmly established at present.

Marine POC in temperate shelf and open estuarine waters has a fairly narrow range of reported carbon isotope compositions, between -18 and $-24‰$ with an overall average of about $-21‰$ (Deuser 1970; Haines and Montague 1979; Tan and Strain 1983; Gearing, Gearing, Rudnick, Requejo, and Hutchins 1984). Exceptions to this generalization occur, however. Blooms of blue-green algae off Florida and in the Gulf of Mexico can have less negative $\delta^{13}C$ values of -12.8 to $-16.8‰$ (Craig 1953, Sackett and Thompson 1963, Fry and Parker 1979). In colder Antarctic waters, in contrast, $\delta^{13}C$ values can be quite negative (to $-31‰$) for mixed phytoplankton/zooplankton samples (Sackett, Eckelmann, Bender, and Be 1965; Sackett *et al.* 1966; Eadie 1972). A temperature dependence of plankton $\delta^{13}C$ values has been suggested (Sacket *et al.* 1965, Fontugne and Duplessy 1981) but not proven (Fontugne and Duplessy 1978; Fry, Anderson, Entzeroth, Byrd, and Parker 1984). Species composition may be a more important controlling factor than temperature (Wong and Sackett 1978; Rau, Sweeney, and Kaplan 1982), as specific groups of marine phytoplankton may show significant differences in their carbon isotope ratio. For example, in Narragansett Bay, Rhode Island, Gearing *et al.* (1984) found a consistent difference in $\delta^{13}C$ between net plankton, centric diatoms with a mean $\delta^{13}C$ of $-20.3‰$, and nannoplankton, < 10 μm phytoflagellates with a mean $\delta^{13}C$ of $-22.2‰$.

POC from brackish and fresh waters can have more negative $\delta^{13}C$ values than oceanic POC. In more confined regions of estuaries, in upper parts of estuaries, and in rivers, phytoplankton should have ^{13}C-depleted values when they utilize ^{13}C-depleted CO_2 produced by respiration of organic carbon. Stable carbon isotope compositions in the range of $-24‰$ to $-30‰$ have been reported for estuarine and riverine POC (Spiker and Schemel 1979,

Sherr 1982, Tan and Strain 1983). Terrestrial C_3 detritus ($\delta^{13}C = -26‰$) may contribute to these more negative $\delta^{13}C$ values.

3.2.4. Autotrophic Bacteria

Peterson, Howarth, Lipschultz, and Ashendorf (1980) calculated the carbon isotope ratios of several autotrophic bacteria from previously published values of the fractionation of ^{13}C and ^{12}C observed in laboratory cultures (Sirevag, Buchanan, Berry, and Troughton 1977; Degens *et al.* 1968b), assuming the source CO_2 had a $\delta^{13}C$ of $-7‰$. The green photosynthetic bacterium *Chlorobium thiosulfatophilum* had a $\delta^{13}C$ of $-20‰$, and the purple photosynthetic bacteria *Rhodospirillum rubrum* and *Chromatium* spp. had $\delta^{13}C$ values between -26 and $-30‰$. A marine chemoautotroph, *Nitrobacter* sp., showed even more depleted isotope values of -34 to $-37‰$. Wong *et al.* (1975) also reported a $\delta^{13}C$ of $-37.5‰$ for the photosynthetic bacterium *Chromatium vinosum* in culture under conditions of non-limiting CO_2 and a $\delta^{13}C$ of $-6.6‰$. Zyakun, Bondar, and Namsaraev (1981) reported that methane-oxidizing bacteria have $\delta^{13}C$ values 10–20‰ more negative than methane so that cell biomass values reach $-64‰$ (methane $\delta^{13}C = -52‰$).

Less is known about the $\delta^{13}C$ values of field populations of autotrophic bacteria. Spies and Des Marais (1983) found a value of $-20.7‰$ for colorless sulfur-oxidizing bacteria, *Beggiatoa* sp. Rau and Hedges (1979) inferred an isotope ratio of about $-33‰$ for chemoautotrophic bacteria in hydrothermal vents of the Galapagos Rift from the stable isotope composition of mussels growing in the vents. In sediments, fluctuations in the total amount and isotopic compositions of porewater DIC will be important in determining $\delta^{13}C$ values of autotrophic bacteria; $\delta^{13}C$ values of porewater DIC can vary greatly over at least a -30 to $+15‰$ range (Anderson and Arthur 1983).

3.2.5. Peat Beds and Soils

Eroding peat beds and soils can be important sources of organic matter in some locations. Depending on the original C_4 or C_3 plant material which formed these deposits, such material may have $\delta^{13}C$ values ranging from $-11.6‰$ (Emery, Wigley, Bartlett, Rubin, and Barghoorn 1967; Brinson and Matson 1983) to $-28.8‰$ (Hunt 1970, Schell 1983).

4. SEDIMENTS AND PARTICULATE ORGANIC CARBON

For estuarine and near-shore shelf systems that have only two major sources of organic carbon, it is often possible to detect the origins of POC and organic matter present in sediments via $\delta^{13}C$ analysis. Such systems include seagrass beds (Fry *et al.* 1977, Thayer *et al.* 1978), salt marshes (Haines and Montague 1979), river mouths (Hunt 1970), and areas polluted by anthropogenic wastes (Botello, Mandelli, Macko, and Parker 1980; Burnett and

Schaeffer 1980; Sweeney *et al.* 1980), petrochemicals (Calder and Parker 1968, Spies and DesMarais 1983), and pulp-mill effluents (Rashid and Reinson 1979). In such cases the carbon isotope composition of POC and organic matter in sediments appears to be a mixture of two major sources of fixed carbon—vascular plants, sewage, oil, or other effluents on one hand, and marine phytoplankton on the other—with varying percentages of each, depending on proximity to the carbon source. Studies of terrestrial *vs.* marine inputs have been most frequently made.

While the difference in stable carbon isotope composition between C_3-dominated terrestrial plant material ($\delta^{13}C$ of $\sim -26‰$) and organic matter of marine origin (*i.e.*, phytoplankton photosynthesis; $\delta^{13}C$ of $\sim -21‰$) is fairly small (5‰), analyses of samples collected along riverine-offshore transects reveal very consistent and similar patterns of isotopic change from terrestrial to marine values. Such transect studies have been carried out in the Gulf of Mexico (Sackett and Thompson 1963; Hedges and Parker 1976; Shultz and Calder 1976; Gearing, Plucker, and Parker 1977; Botello *et al.* 1980); in the St. Lawrence Estuary, Canada (Pocklington 1976; Tan and Strain 1979a,b, 1983); in U.S. Atlantic estuaries (Hunt 1970, Burnett and Schaeffer 1980, Sherr 1982, Brinson and Matson 1983, Gearing *et al.* 1984); off southern California (Nissenbaum and Kaplan 1972); in San Francisco Bay (Spiker and Schemel 1979); and in several European estuaries (Letolle and Martin 1970, Salomons and Mook 1981). In these studies the transition to marine values of $-21‰$ typically occurs fairly sharply near river mouths (Hunt 1970). The general conclusion of these investigations is that there is little influence of river-introduced organic carbon beyond the freshwater and brackish-water regions of estuaries. In cases where there is a large volume flow of water, as for the Mississippi River, the "estuarine area" influenced by terrestrial carbon may extend out for some distance onto the near-shore shelf (*e.g.*, Schultz and Calder 1976, Gearing *et al.* 1977). In view of the consistent changes found along transects, simple two-source mixing models (Fig. 1A) have often been used to calculate the relative importance of marine and terrestrial carbon sources for points along the transects.

These mixing models are open to several criticisms. The first is that calculating the importance of various sources is severely dependent on the exact $\delta^{13}C$ values used for the sources. For example, in a study tracing the downstream fate of pulp mill effluent, Rashid and Reinson (1979) used -27.5 and $-18‰$ as $\delta^{13}C$ values representative of terrestrial and marine organic matter, respectively. A value of $-22.7‰$ would represent a 50/50 mixture if only these two sources were involved. However, if a more usual $-21‰$ value were assumed for marine organic matter, rather than $-18‰$, the $-22.7‰$ value would indicate that $\sim 75\%$ of the sedimentary organic carbon was marine in origin. Because such percentage calculations depend strongly upon specific assumptions about source $\delta^{13}C$, each study should clearly identify and explain $\delta^{13}C$ values chosen for the local sources used in mixing models.

Terrestrial *vs.* marine mixing models are open to two other potential

complications whose importance may vary from system to system. These potential complications are 1) isotopic changes in plant source material due to heterotrophic metabolism during decomposition processes, and 2) overlooked sources of *in situ* carbon production that have $\delta^{13}C$ values similar to phytoplankton or terrestrial plants.

Significant $\delta^{13}C$ changes of more than 2‰ during either aerobic and anaerobic decomposition of plants have not been generally observed. Several laboratory studies have followed $\delta^{13}C$ in decomposing vascular plant material and have shown only minor changes in carbon isotope composition of the plant material over many months of degradation (Haines 1977, Schwinghamer *et al.* 1983, Stephenson, personal communication). *In situ* humic matter also seems to closely mirror the $\delta^{13}C$ of fresh source plant carbon (Nissenbaum and Kaplan 1972, Eadie and Jeffrey 1973, Johnson and Calder 1973). However, Hayes, Kaplan and Wedeking (1983) suggest that over geologic times, ^{13}C-depleted carbon is lost from kerogens (isotopic discrimination = −2.7‰).

A variety of potential autotrophic carbon sources should also be considered before interpreting $\delta^{13}C$ values of coastal sediments and seston. For example, Brinson and Matson (1983) have presented evidence that the more negative $\delta^{13}C$ values in upper estuaries (−24 to −27‰) in fact result in large part from *in situ* phytoplankton production rather than from C_3 plant litter. Tan and Strain (1983) also consider the more negative particulate organic carbon in the Upper St. Lawrence estuary to be predominantly of phytoplankton origin. The more negative −27‰ $\delta^{13}C$ values attributed to terrestrial materials in marine *vs.* terrestrial mixing studies (see above) may indicate phytoplankton inputs in some locations. This situation is likely to be most important in the upper reaches of estuaries where DIC values can reach values of −10‰ and phytoplankton values may decrease from oceanic −21‰ values to −30‰.

A last general problem for carbon isotope studies of POC and organic matter in sediments is the multiple source problem outlined in Fig. 1C. For instance, in Georgia salt marsh estuaries, $\delta^{13}C$ values of seston and sedimentary organic matter range between −17‰ and −24‰. Five sources are of potential importance in this system: −13‰ *Spartina*, −17‰ benthic microalgae, −21‰ phytoplankton, −26‰ terrestrial plant litter, and −20‰ to −30‰ autotrophic sulfur-oxidizing bacteria (Haines 1977; Peterson, Howarth, Lipschultz, and Ashendorf 1980; Sherr 1982). The −17 to −24‰ values for POC and sedimentary organic carbon could indicate several combinations of source materials, although the values are sufficiently negative to indicate at most only a moderate importance for *Spartina*. In this and other multi-source examples, $\delta^{13}C$ studies alone cannot accurately resolve all source contributions but do provide constraints about the maximum importance of especially the two "end-member" sources with the extreme isotopic values.

Despite the problems of interpretation of $\delta^{13}C$ values discussed above, the reported values for the stable carbon isotope composition of POC and

organic matter in sediments in a variety of estuarine and near-shore systems usually lie within a fairly narrow −20 to −27‰ range (Table 2). This may be

TABLE 2

$\delta^{13}C$ values of particulate organic carbon (POC) and sedimentary organic matter in several estuaries.

Site	$\delta^{13}C$ POC	$\delta^{13}C$ Surface Sediments	Reference
Gulf of St. Lawrence:			Tan and Strain 1979b
Surface water	-24.9 ± 0.5		
Deep water	-26.2 ± 1.0	-22.4 ± 0.2	
Pamlico River Estuary, North Carolina	-21 to -25	-23 to -26	Brinson and Matson 1983
St. Louis Bay, Mississippi	-25 to -26.7	-20.7 to -23.2	Hackney and Haines 1980
San Francisco Bay	-22 to -26	-24	Spiker and Schemel 1979
Georgia salt marsh estuary	-24.5 ± 1.7	-21.1 ± 2.4	Sherr 1982
Pecks Cove, Bay of Fundy	-21.1	-20.3	Schwinghamer *et al.* 1983
Narragansett Bay, Rhode Island	-20 to -22	-21.5 ± 0.5	Gearing *et al.* 1984
Coastal Lagoons, Gulf of Mexico	---	-20.1 to -23.9	Botello *et al.*, 1980
Laguna Madre, Texas	---	-14 to -19.5	Fry *et al.* 1977

due to a long-term "averaging out" of all the source material $\delta^{13}C$ values in the system or to phytoplankton production being the dominant source of organic carbon in most coastal environments, as suggested by Brinson and Matson (1983). Exceptional −14 to −19.5‰ values are found in the Laguna Madre of Texas where large seagrass meadows occur (Fry *et al.* 1977). There are frequently small but consistent differences in $\delta^{13}C$ between POC and sediment (Table 2). These differences have been ascribed either to isotope effects accompanying bacterial metabolism in surface sediments (Eadie and Jeffrey 1973) or to a greater influence of refractory vascular plant material in sediments as compared to POC: *e.g.*, *Spartina* detritus in Georgia estuaries (Sherr 1982) or C_3 terrestrial plant material in San Francisco Bay (Spiker and Schemel 1979).

In summary, it appears that the use of $\delta^{13}C$ to determine the origins of organic matter in coastal waters can only provide an unequivocal answer when there are no more than two sources of organic carbon whose $\delta^{13}C$ values are precisely known and relatively constant. The situation which most closely meets these requirements is one of point influx of an organic pollutant into a system dominated by phytoplankton production. However, stable carbon isotope analysis can be a valuable addition to studies involving multiple approaches to elucidating sources of organic seston and sediment (*e.g.*, Peters, Sweeney, and Kaplan 1978; Sweeney *et al.* 1980; Macko 1983).

5. FOOD WEBS

5.1. THE ISOTOPIC RESEMBLANCE OF ANIMALS AND MICROBIAL HETEROTROPHS TO THEIR DIETS

To apply mixing models (Fig. 1) to food web ecology, many studies have

tested the isotopic similarity between consumers and their foods. Animals usually have $\delta^{13}C$ values within ± 2‰ of their foods, as do most microbial heterotrophs (Fig. 3). Notable exceptions have been found in some microbial

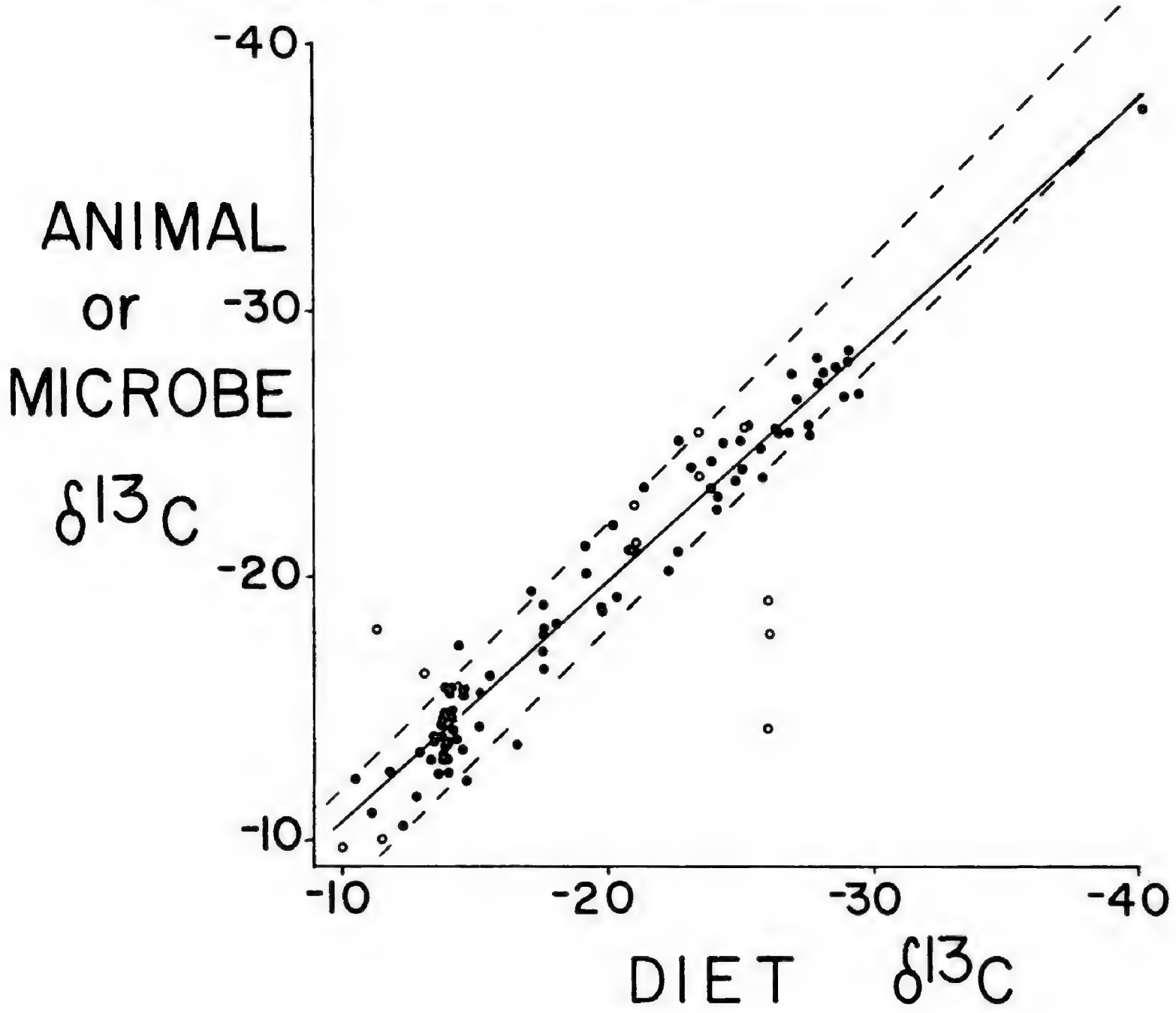

FIG. 3. Relationship between organismal and dietary values for animals (•) and microbes (o). Best-fit line (method of least squares) for animal data only is $Y = 0.904X - 1.68$ ($n = 83$). Confidence limits (95%) for the slope = ± 0.046. Dashed lines are $Y = X + 2$ and $Y = X - 2$; most points fall between these lines, showing that animals usually have $\delta^{13}C$ values within ± 2‰ of their diets. Data compiled from field and laboratory studies in which the diet or carbon source was well-known; individual data were averaged when given. Animals: Fry 1977, DeNiro and Epstein 1978, Fry *et al.* 1978, Haines and Montague 1979, Petelle *et al.* 1979, Teeri and Schoeller 1979, Rau and Anderson 1981, Fry and Arnold 1982, Macko *et al.* 1982, unpublished data. Microbes: Abelson and Hoering 1961, Jacobson *et al.* 1970, Whelan 1971, Ingram *et al.* 1973, Barghoorn *et al.* 1977, Monson and Hayes 1980, Ivlev *et al.* 1982.

studies. Photosynthetic bacteria grown under photoheterotrophic conditions on succinate had $\delta^{13}C$ values 7–12‰ less negative than the succinate, although when grown on yeast extract this difference diminished to more usual 0.2–1.7‰ values (Barghoorn *et al.* 1977). To explain the large

discrepancy in the case of succinate, Barghoorn *et al.* speculated that the succinate was not isotopically homogeneous. At the other extreme of isotopic disagreement, Ivlev, Kaloshin, Radyukin, Sholin, and Pozdnyakova (1982) found that a threonine-excreting mutant strain of *E. coli* had $\delta^{13}C$ values of cells that were 6.7‰ more negative than the glucose substrate. It should be noted, however, that Abelson and Hoering (1961) and Monson and Hayes (1982) report more usual 0.3–1.9‰ differences for non-mutagenized strains of *E. coli* grown on glucose. Macko and Estep (1983) found that cells of the bacterium *Vibrio harveyii* ranged in $\delta^{13}C$ from −5.5 to +11.1‰ relative to amino acids used as growth substrates. The larger 3–11‰ differences between cells and amino acid carbon sources may have been due to isotopic heterogeneities among individual carbon atoms in the amino acids (Macko and Estep 1983). In most studies, close isotopic similarities of animals and heterotrophic bacteria to their diets are observed (Fig. 3). This similarity basically holds because isotopic fractionations during assimilation and respiration are small (Mosora, Lacroix, and Duchesne 1971a; DeNiro and Epstein 1978; Fry *et al.* 1984). Linear regression (Fig. 3) indicates that over the −10 to −24‰ range commonly encountered among marine animals, animal $\delta^{13}C$ values do, on average, resemble dietary values within ± 0.7‰. This level of uncertainty is small but appreciable when compared to the 5–13‰ differences typically found between food resources (*e.g.*, Fig. 1A).

While heterotrophs generally bear a close isotopic resemblance to their diets, considerable isotopic fractionation can still occur in heterotrophic metabolism. Thus, biochemical fractions such as lipids and proteins or tissues such as fat and muscle can have $\delta^{13}C$ values that differ by > 2‰ (Parker 1964; van der Merwe 1982). Dietary relationships shown in Fig. 3 were established by homogenizing whole animals or microbes for determination of heterotrophic $\delta^{13}C$; muscle tissue, which often constitutes a major portion of an animal's body mass, is a commonly subsampled substitute in field studies dealing with large animals. Because animals obtain essential amino acids from their diets, analyses of these acids may show a closer animal-diet $\delta^{13}C$ similarity than analyses of whole tissues or animals. (Macko, Estep, Hare, and Hoering 1983a give methods for isolation and isotopic analysis of individual amino acids.)

Sources of variability important for evaluating results of mixing models include individual and between-species variations in animal $\delta^{13}C$ in relation to diet. Isotopic studies of animals fed the same diet report a relatively small 1–2‰ $\delta^{13}C$ variation among individuals (Fry 1977, DeNiro and Epstein 1978, Fry and Arnold 1982). Field studies often show comparable small intraspecific ranges (Fry *et al.* 1978; Haines and Montague 1979; Stephenson and Lyon 1982); a remarkably low 0.7‰ range has been reported for 41 specimens of an offshore benthic fish (Fry and Parker 1979). Different species of animals fed the same laboratory diet also have similar $\delta^{13}C$ values within 1‰ (DeNiro and Epstein 1978). Close agreement of $\delta^{13}C$ values between different species has also been observed in field collections of bivalves (Incze *et al.* 1982) and offshore benthic crustaceans (Fry 1981a).

These small ranges among individuals and close similarities among species suggest that a relatively small sampling effort should be sufficient to characterize average $\delta^{13}C$ values of many consumers. Detailed studies of the range of individual variation, however, can yield useful information about dietary variation among individuals (Parker 1964, Fry *et al.* 1978).

Isotopic data can also be useful for identifying animals that are switching diets. Mosora *et al.* (1971a) used laboratory rats to follow isotopic changes when a new glucose diet +12.5‰ enriched in ^{13}C was substituted for the standard laboratory feed. For young, one-week-old rats, $\delta^{13}C$ values of respired CO_2 changed within one day to +11‰ (*vs.* the old laboratory diet), reflecting the switch to the new diet. This isotopic change was slower in adult animals. Analysis of tissues after 25 days on the new diet showed that the greatest isotopic change (turnover) had occurred in the liver, while fur and bone showed the least change (Mosora *et al.* 1971a, Lacroix and Mosora 1975). Isotopic diet-switching laboratory experiments have also been reported for crabs, shrimp, and gerbils (Haines and Montague 1979; Fry and Arnold 1982; Tieszen, Boutton, Tesdahl, and Slade 1983), and several field examples have been documented (Fry 1981a, Schell 1983, Fry 1984b). Tieszen *et al.* (1983) have suggested that analysis of tissues that have slow and fast turnover rates can identify (1) animals that are switching to an isotopically novel diet, and (2) the average isotopic composition of an animal's diet over the long term (slow turnover tissues) and short term (fast turnover tissues).

5.2. $\delta^{13}C$ ENRICHMENT IN OFFSHORE FOOD WEBS

Although laboratory and field studies have shown small fractionations associated with one trophic level (Fig. 3), no laboratory studies have been made that examine isotopic fractionations in complex food webs such as those found in nature. Offshore food webs have been suggested as appropriate natural examples in which cumulative fractionation patterns can be studied (McConnaughey and McRoy 1979a, Rau *et al.* 1983). This suggestion is based on the considerations that phytoplankton (measured as POC) at the base of the food web has fairly constant isotopic values averaging about −21‰ in many oceans and that phytoplankton are the sole source of fixed carbon.

Offshore studies uniformly show that substantial ^{13}C enrichments occur in natural food webs and that a regular progression occurs toward less negative $\delta^{13}C$ values from POC to benthic consumers (Table 3; Fig. 4). Overall, maximal ^{13}C enrichments are 7.4–9.0‰ in these food webs (Fig. 4). Variations in ^{13}C enrichment patterns (Fig. 4) probably arise from the high variability in $\delta^{13}C$ values of POC and low number of analyses (N = 1 to 4 for POC in all offshore ecosystems except the Gulf of Mexico, Table 3). In the offshore Gulf of Mexico where sampling has been most complete, ^{13}C enrichment: (1) is consistently observed in different seasons and locations, and (2) occurs in deeper waters which are little influenced by possible

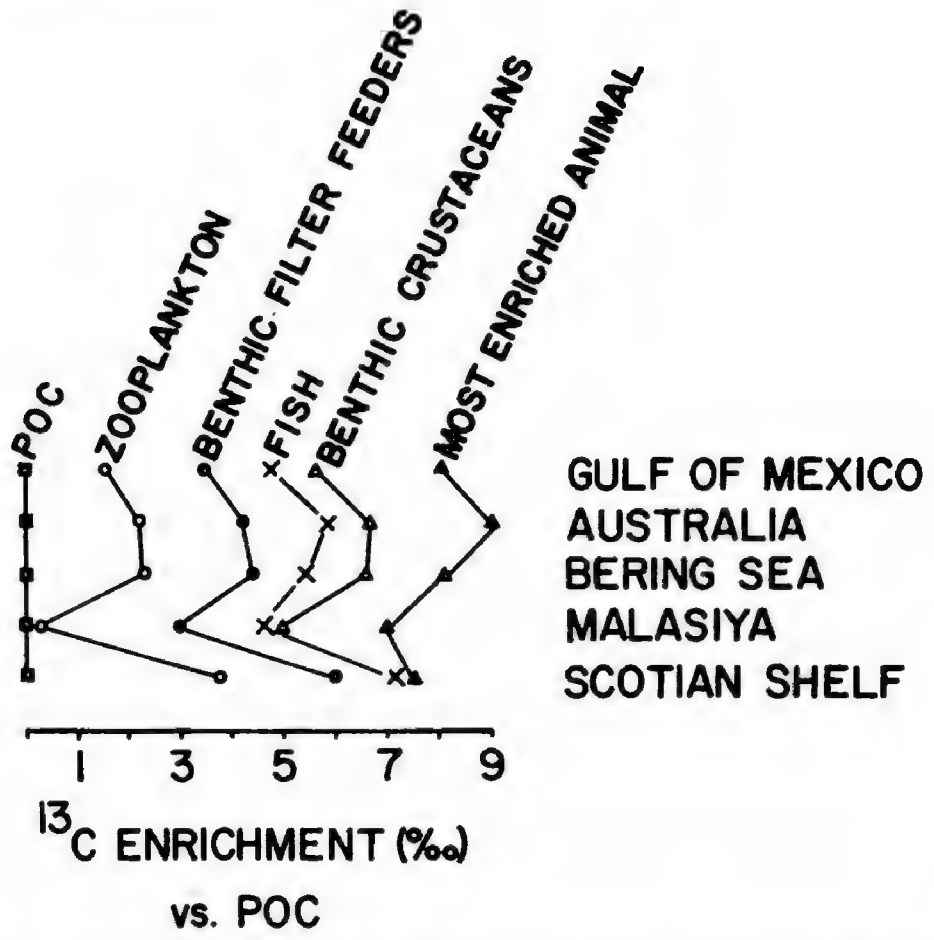

FIG. 4. Animal ^{13}C enrichment in five offshore ecosystems expressed as ‰ increase *vs.* $\delta^{13}C$ value of particulate organic carbon (POC). ‰ ^{13}C enrichment = animal $\delta^{13}C$ − POC $\delta^{13}C$. Data taken from Table 3.

TABLE 3

^{13}C Enrichment in offshore food webs. Mean $\delta^{13}C \pm$ S. D. (*N*).

	South Indian (Antarctic) Ocean [a]	Scotian Shelf [b]	Bering Sea [c]	Torres Strait, Australia [d]	Straits of Malacca, Malaysia [e]	Gulf of Mexico [f]
Particulate organic carbon (POC)	---	-25.3 ± 2.8 (4)	-24.4 (1)	-21.8 ± 0.9 (2)	-21.2 (1)	-21.7 ± 1.6 (87)
Zooplankton	-26.4 ± 1.5 (12)	-21.5 ± 1.1 (8)	-22.1 (1)	-19.6 ± 1.8 (8)	-20.9 (1)	-20.2 ± 1.4 (63)
Benthic filter feeders	-21.4 (1)	-19.3 (1)	-20.0 ± 0.9 (4)	-17.6 ± 1.3 (2)	-18.2 ± 0.6 (3)	-18.2 ± 0.6 (3)
Fish	---	-18.1 ± 0.5 (2)	-19.0 [g] ± 1.3 (6)	-15.9 ± 1.4 (44)	-16.6 (1)	-17.0 ± 1.0 (54)
Benthic crustaceans	---	---	-17.8 ± 1.0 (6)	-15.1 ± 0.7 (14)	-16.2 ± 0.8 (22)	-16.1 ± 0.2 (138)
Greatest ^{13}C enrichment	-18.7 benthic polychaete	-17.8 benthic fish	-16.3 benthic gastropod	-12.8 [h] benthic holothurian	-14.2 benthic gastropod	-13.7 benthic gastropod

[a] Eadie 1972.
[b] Mills *et al.* 1983.
[c] McConnaughey and McRoy 1979a.
[d] Fry *et al.* 1983.
[e] Rodelli 1981.
[f] Combined data from Sackett and Thompson (1963), Calder (1969), Eadie and Jeffry (1973), Gormaly and Sackett (1977), Fry (1977), Eadie *et al.* (1978), Fry and Parker (1979), Fry *et al.* (1984).
[g] One -24.1 o/oo lipid-rich bathypelagic fish has been excluded from this average.
[h] One -10.8 o/oo fish was also found, but this mobile animal may have been feeding on reefs in the area.

carbon inputs from land (Fry *et al.* 1984). While other studies have measured only a few consumers in offshore food webs (*e.g.*, Rau *et al.* 1981; Chisholm *et al.* 1982), they support the data presented in Table 3; $\delta^{13}C$ values of fish and benthic crustaceans in temperate and tropical oceans usually average less negative than −18‰ and are thus enriched in ^{13}C relative to −21‰ POC.

Taken together, the ^{13}C enrichments observed offshore suggest that along with diet, trophic position exerts a major influence on the carbon isotopic values of animals. McConnaughey and McRoy (1979a) derived a preliminary estimate of 1.5‰ ^{13}C enrichment per trophic level in a study of Bering Sea fauna. Rau *et al.* (1983) have recently refined this estimate to 0.7 to 1.4‰; their study compared muscle tissue from consumers whose trophic level was defined by careful analyses of stomach contents. However, $\delta^{13}C$ values did not always show a consistent $\delta^{13}C$ enrichment with increasing trophic level. For example, isotopic values for skipjack and yellowfin tuna were identical (Rau *et al.* 1983), but other evidence (Cs/K ratios and gut content analyses) indicated that yellowfin occupied a considerably higher trophic level than skipjack (Olson 1983). This lack of consistency in ^{13}C enrichment factors (0, 0.7, 1.4, or 1.5‰) makes it difficult to model food web structure using $\delta^{13}C$ data, although for some purposes an average increase of 1‰ per trophic level may suffice.

Establishing the exact magnitude of the ^{13}C increase can be quite important if accurate corrections are to be made in mixing models (Fig. 1B). As studies of zooplankton show, establishing a satisfactory correction factor can be difficult, and in fact, contradictory results have been reported. For instance, Tan and Strain (1983) found essentially no ^{13}C enrichment of net plankton relative to POC in the Gulf of St. Lawrence. Earlier reports agree in principle with this result, as plankton samples dominated by zooplankton or phytoplankton had very similar values (Sackett *et al.* 1965, Degens *et al.* 1968a, Deuser 1970). However, Thayer, Govoni, and Connally (1983) found consistent 0.8–2.2‰ ^{13}C enrichments for total zooplankton or copepods *vs.* phytoplankton in the offshore Gulf of Mexico. More extensive sampling in the northwestern Gulf of Mexico suggests a third and variable relationship between POC and zooplankton (Fry *et al.* 1984). Zooplankton was similar to POC in the −18 to −20‰ range, but enriched by 2–4‰ at −24‰ values of POC (Fry *et al.* 1984). Given these disagreements, future studies should examine POC more closely in terms of assimilable components and species composition. Incze *et al.* (1982) have argued that POC consists of "labile" and "refractory" components that differ in isotopic values. Assimilation of labile living phytoplankton components could perhaps account for the variable ^{13}C enrichments observed in estuarine bivalves *vs.* total POC (Stephenson and Lyon 1982, Incze *et al.* 1982). In the open ocean there is some evidence that more refractory components of POC have more negative values: detrital POC collected in deep mid-water samples often has $\delta^{13}C$ values more negative than surface POC (Eadie and Jeffry 1973; Eadie *et al.* 1978), but not always (Calder 1969, Williams and Gordon 1970, Edmond *et al.* 1981). Species composition and growth conditions can also affect $\delta^{13}C$ values of

phytoplankton and POC (Degens *et al.* 1968b; Pardue *et al.* 1976; Estep, Tabita and Van Baalen 1978b; Wong and Sackett 1978). Species composition may also be important in determining $\delta^{13}C$ values of zooplankton populations, especially when individual species feed at different trophic levels (Thayer *et al.* 1983, Mills *et al.* 1983). In view of such complicating factors, careful studies are needed before exact ^{13}C enrichment factors can be specified for zooplankton and other offshore consumers.

Examining $\delta^{13}C$ values of bathypelagic midwater organisms may reveal much about causes of ^{13}C enrichment observed offshore. McConnaughey and McRoy (1979a) have argued that the largest ^{13}C enrichments observed offshore, those in benthic animals (Table 3), are due to microbial and meiofaunal reworking of planktonic carbon in sediments. This would add one or more trophic levels to benthic food chains. No tests have been made of this hypothesis, although preliminary data on bathypelagic animals that have a weak trophic link to sediments show a much decreased ^{13}C enrichment. Williams and Gordon (1970) found -18 to $-20.3‰$ values for bathypelagic fish and crustaceans from the Pacific and essentially no ^{13}C enrichment relative to two samples of surface zooplankton. Also, bathypelagic shrimp and fish collected in the Caribbean had fairly negative -18 to $-19‰$ values (Fry *et al.* 1982a) indicating a small ^{13}C enrichment relative to surface POC, which may average near $-21‰$ in this region (Eadie and Jeffrey 1973). These preliminary results are thus consistent with the idea that the larger ^{13}C enrichments observed in benthic animals on continental shelves (Table 3) are caused by an increased number of trophic levels in sediment-linked food webs.

Both selective ^{12}C loss via respiration and selective assimilation of ^{13}C-enriched foods have been suggested as mechanisms that could account for the progressive ^{13}C enrichments observed in offshore food webs (McConnaughey and McRoy 1979a, Fry 1981b). Evidence for selective loss of $^{12}CO_2$ during respiration is based on small ($< 1‰$) isotopic differences of respired CO_2 *vs.* diet for three of four laboratory-grown terrestrial animals (DeNiro and Epstein 1978). Earlier studies have shown even smaller differences for CO_2 *vs.* diet for undisturbed terrestrial animals ($< 0.3‰$; Mosora *et al.* 1971a), although larger differences were observed following injections of various hormones (Mosora *et al.* 1971b, 1972). Selective assimilation of ^{13}C-enriched components in natural diets has been demonstrated for offshore shrimp (Fry *et al.* 1984); assimilated materials averaged $+1.3‰$ relative to total stomach contents. Selective assimilation could account for the ^{13}C enrichment of offshore shrimp *vs.* their natural diets without invoking selective loss of respired $^{12}CO_2$ (Fry 1981b).

5.3. ESTUARINE FOOD WEBS

Stable isotope studies of estuarine food webs have focused on identifying which plant foods supply most carbon to consumers. This task has been complicated by the near-continuous distribution of $\delta^{13}C$ values among marine plants. Initial hypotheses considered only two sets of dietary plants

whose $\delta^{13}C$ values were well-separated—*e.g.*, −10‰ seagrasses *vs.* −21‰ phytoplankton, or −13‰ *Spartina vs.* −27‰C_3 terrestrial plants—yet common benthic micro- and macroalgae proved to have intermediate values between these groups (Smith and Epstein 1971, Haines 1976b, DeNiro and Epstein 1981b, Fry *et al.* 1982a, Fry *et al.* 1983b). Consequently, animals displaying intermediate $\delta^{13}C$ values may be consuming any of several mixed or pure diets; unambiguous interpretation of such values is not possible (Fig. 1C).

Two comparative approaches have been adopted to partially circumvent these difficulties. First, $\delta^{13}C$ values of animals collected in seagrass meadows have been compared with isotopic values of offshore animals (Parker and Calder 1970, Fry and Parker 1979, McConnaughey and McRoy 1979b). Animals feeding offshore ultimately rely on phytoplankton carbon, while food webs in seagrass meadows have additional, ^{13}C-enriched carbon sources in benthic seagrasses and algae. Animals from seagrass meadows should be enriched in ^{13}C relative to offshore animals if benthic plants are important additional sources of dietary carbon in seagrass meadows. A second approach has been to compare animals in neighboring marshes which differ in the isotopic composition of the dominant macrophyte (Haines 1976a, Hackney and Haines 1980, Hughes and Sherr 1983). Animals consuming large amounts of macrophyte-derived material should show large isotopic differences between the two areas, while animals consuming other phytoplankton or benthic algal foods should show small differences. A related strategy recently employed in trophic investigations of epiphytic algae in south Texas seagrass meadows (Kitting *et al.* 1984) is to compare consumers in areas where epiphyte values differ but seagrass values are the same. Animals consuming epiphytes should show isotopic changes that parallel changes in epiphyte $\delta^{13}C$ in the different study areas but that are not closely linked to $\delta^{13}C$ values of seagrasses. However, all these comparative approaches rely on the concept of a controlled experiment in which overall food web dynamics (productivities, trophic levels, etc.) remain similar, and only isotopic compositions of plant sources vary. This will not be strictly true for many field situations.

5.3.1 Seagrass Meadows

Comparison of faunal $\delta^{13}C$ values from seagrass meadows in northern Australia, the Caribbean, south Texas, Alaska, North Carolina, and Florida shows considerable isotopic variation (Table 4). This variation occurs even though $\delta^{13}C$ values of POC and the dominant seagrasses are roughly constant within ± 2‰. Based on isotopic values for benthic-feeding shrimp, crabs, polychaetes, holothurians, and gastropods, the seven seagrass meadows of Table 4 may be broadly classified into three categories: high (meadow 1), intermediate (meadows 2–5), and low or no (meadows 6 and 7) faunal ^{13}C enrichment relative to offshore fauna. Animals in four other seagrass meadows not listed in Table 4 show intermediate ^{13}C enrichments *vs.* offshore animals: Izembeck Lagoon, Alaska (McConnaughey and McRoy

TABLE 4

Average $\delta^{13}C$ values in seven seagrass meadows and the offshore Gulf of Mexico.

	Seagrass Meadows							Offshore
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	Gulf of Mexico
Particulate Organic Carbon	---[a]	---[a]	---[a]	---[b]	-20.7	-19.4	-21.6	-21.7
Dominant seagrass	- 8.6	-9.4	- 8.6	-11.5	-10.0	-10.3	- 8.0	---
Seagrass Epiphytes	-11.1[c]	---	-14.0	-12.4	-14.4[c]	-16.0	-19.3	---
Zooplankton	-18.5[c]	-16.8[c]	-17.2[c]	-16.0[c]	---	---	-18.4	-20.2
Other filter feeders (bivalves, barnacles, sponges)	-15.6[c]	-16.0[c]	-14.8[c]	-18.1	-15.3	-18.3	-19.2	-18.2
Leaf epifauna	-10.8[c]	---	-18.6[c]	---	---	-15.1	-20.4	---
Fish	- 8.4	-14.1	-13.6	-12.8	-12.1	-16.8	-17.2	-17.0
Shrimp	- 7.4[c]	- 9.7[c]	-12.7[c]	-11.3[c]	-12.7	-15.6[c]	-17.9	-16.1
Crabs	- 8.2	-12.1	-12.6	-12.2[c]	-10.7	---	---	-15.3
Infaunal polychaetes	- 9.3[c]	---	-11.5	-11.9	-13.1	---	-16.4	-17.8
Holothurians	- 6.6	---	- 6.4[c]	-11.8[c]	---	---	---	-14.3[d]
Benthic gastropods	-6.2	-15.4	-12.0	-15.4	---	-14.6[c]	---	-14.1

Seagrass meadows 1-7 are: 13 = Bampfield Head, Friday Passage, and Battery Point, Australia (Fry *et al.* 1983 b); 4 = St. Croix and Nicaragua (Fry *et al.* 1982 a); 5 = Upper Laguna Madre, Texas (Fry 1977, Fry and Parker 1979, unpublished data); 6 = Phillips Island, North Carolina (Thayer *et al.* 1978); 7 = Inndian River Lagoon, Florida (Fry 1984a).

[a] POC collected outside this seagrass meadow averaged -21.8 o/oo.
[b] POC collected outside these seagrass meadows averaged -20.8 (Land *et al.* 1977).
[c] One or two samples only included in average value.
[d] Average of values from Torres Strait, Australia.

1979b), Redfish Bay, Texas (Parker 1964), and Miami and Long Key, Florida (Craig 1953).

The intermediate ^{13}C enrichments observed in most seagrass meadows have led to the conclusion that food webs in seagrass meadows are partially based on ^{13}C-enriched benthic plants. Estimates of the carbon contributions made to food webs of seagrass meadows by benthic plants span a 0–100% range but are commonly > 50% (Thayer *et al.* 1978, McConnaughey and McRoy 1979b, Fry and Parker 1979, Fry *et al.* 1982a, Fry *et al.* 1983b). However, determining which of the benthic plants—seagrasses, seagrass epiphytes, epibenthic microalgae, or macroscopic drift algae—are in fact most important for grass flat food webs has been much more difficult. For instance, only in seagrass meadow 1 (Table 4) do benthic consumers have $\delta^{13}C$ values enriched in ^{13}C relative to seagrasses. On the basis of offshore studies reviewed above such ^{13}C enrichments are expected if seagrasses are the source of most carbon in grass flat food webs. The more negative $\delta^{13}C$ values observed in most seagrass meadows could alternatively indicate that seagrass "and microalgal carbon become mixed early in the food web by a variety of organisms" (McConnaughey and McRoy 1979b). On the basis of productivity, feeding behavioral, and isotopic studies, Kitting *et al.* (1984) suggest that seagrass epiphytes are an important carbon source for consum-

ers in grassflats. Isotopic evidence alone does not contradict this view, as faunal $\delta^{13}C$ values in grass flats are similar to those of epiphytes (Table 4), especially when isotopic differences between seagrasses and epiphytes are greatest (meadows 6 and 7, Table 4). Algal contributions have also been hypothesized by Fry *et al.* (1983b) to explain the unusual faunal ^{13}C enrichments observed in seagrass meadow 1 (Table 4). Epibenthic and endolithic -7 to -9‰ ^{13}C-enriched blue-green algae (Calder and Parker 1973, Barghoorn *et al.* 1977, Fry *et al.* 1983b) are probably important carbon sources in this meadow.

5.3.2. Salt Marshes

A salient question in salt marsh ecology is whether food webs in "macrophyte dominated estuaries" are "in large part based on non-living (vascular) plant material" (Haines 1979). Isotopic studies have been focused on this topic, and special interest attached to confirming or disproving the hypothesis that decaying *Spartina alterniflora* is the dominant food source in many salt marshes. For at least some salt marsh animals, isotopic evidence is consistent with a diet based on *Spartina.* Intertidal crabs and snails collected in Georgia *Spartina* marshes show -11 to -16‰ average isotopic values, close to the -13‰ value of *Spartina* (Haines 1976a,b; Haines and Montague 1979. Also killifish collected in North Carolina marshes had -13.9 to -15.8‰ values close to -13‰ (Kneib *et al.* 1980). Evidence for consumption of C_3 marsh plants is weaker. With the exception of some *Uca* fiddler crabs in Altamaha River swamps and marshes (Haines and Montague 1979), animals collected in Georgia marshes (where the $\delta^{13}C$ values of the dominant C_3 plants were about -26‰) did not have $\delta^{13}C$ values close to -26‰; isotopic values of -16 to -21‰ were most common (Haines 1976a, Haines and Montague 1979). Three explanations have been offered for this general lack of approach to -26‰ values in the C_3 marsh fauna: (1) C_3 plants are not as easily assimilated as C_4 *Spartina*; (2) the mobile animals which were sampled may have previously fed in *Spartina* stands or have fed on *Spartina* detritus washed into C_3 stands by tides; or (3) phytoplankton and benthic algae with -16 to -22‰ values are more important food sources in some marsh areas. Analysis of fauna from three subtidal creeks draining C_3 and *Spartina* marshes support the last two alternatives (Hughes and Sherr 1983). Fauna collected in tidal creeks draining *Spartina* ($\delta^{13}C = -13$‰) and *Juncus* ($\delta^{13}C = -26$‰) marshes averaged -17.6 and -20.1‰, respectively. Relative to each other, these averages show some bias toward the $\delta^{13}C$ values of the dominant *Spartina* and *Juncus* plants, which indicates that "vascular marsh plant detritus is a carbon source for the subtidal food web in Georgia estuaries" (Hughes and Sherr 1983). However, the difference between the subtidal averages is fairly small (< 3‰), which suggests that the system is well-buffered with either phytoplankton/benthic algae or a near-equal mixture of C_3 and C_4 plants supplying most carbon to the fauna.

Spartina and *Juncus* marsh fauna were also compared in a Mississippi estuary (Hackney and Haines 1980). As in Georgia, isotopic averages

differed by < 3‰, with averages biased in the direction of the local dominant marsh plant. However, analysis of filter-feeding bivalves in both marshes yielded −26 to −28‰ values, which suggests that terrestrial materials or very negative estuarine algae are imported into both areas. Isotopic values more negative than −20‰ were common in mobile fauna of both areas, also perhaps indicating an increased reliance on imported materials. Import of C_3 plant material was judged to be higher in the Mississippi marshes than in Georgia *Spartina* marshes (Hackney and Haines 1980).

Lastly, a marsh study in Louisiana (Fry 1984b) compared $\delta^{13}C$ values of small shrimp collected in *Spartina* marshes *vs.* open bays of the Barataria Bay region. In this case, no significant differences were found between mean values of shrimp in the two areas (−18.8 in open bays *vs.* −18.9 for *Spartina* marshes) so that a shift toward *Spartina* values was not observed in the *Spartina* marsh samples.

In summary some animals collected in Georgia *Spartina* marshes (Haines and Montague 1979) have $\delta^{13}C$ values near that of *Spartina*. However, isotopic studies of Mississippi and Louisiana marsh fauna show that more negative −18 to −23‰ values are also commonly found in *Spartina* marsh invertebrates. A source of ambiguity in the studies made to date is that the benthic snails, shrimps, crabs, and fish analyzed are all mobile; studies of sessile fauna should more clearly reveal local isotopic patterns within marshes. Very localized patterns do exist. For instance, a tube-dwelling polychaete, *Branchioaschsis americana*, from a 3 m diameter open, unvegetated pool in a Texas bay measured −13.7‰, while 5 m away among roots of surrounding mangroves a polychaete of the same species measured −18.9‰ (Fry 1977). The more negative −18.9‰ value may arise from increased consumption of mangrove leaf litter ($\delta^{13}C = -24.5$‰) that is localized beneath the mangrove plants.

A second problem of these marsh studies lies in the failure of $\delta^{13}C$ values to indicate clearly which plants are important foods for the many marsh animals with −16 to −23‰ values. Two alternate sets of foods could be phytoplankton and benthic algae or a mixture of C_3 and C_4 vascular plant detritus. Algal foods may be important. In Texas bays that have minimal stands of marsh plants compared to Louisiana, Mississippi, or Georgia, −16 to −22‰ values are common among estuarine shrimp (Fry 1981a). Presumably, isotopic values in these open bays reflect a diet derived from estuarine phytoplankton and benthic algae. The study of Hackney and Haines (1980), however, indicates that imported C_3 plant materials or riverine algae may be important carbon sources in some marshes. Other techniques, possibly the combined use of $\delta^{13}C$ and $\delta^{34}S$ values (Peterson and Howarth 1983), are needed to distinguish an algal-based diet from a mixed diet of C_3 and C_4 plants (Haines and Montague 1979) or of benthic microalgae and *Spartina* (Schwinghamer *et al.* 1983). Establishing the importance of C_3 and algal foods in diets will also clarify the role of *Spartina* detritus as a food source for marsh animals.

5.4. FRESHWATER ECOSYSTEMS

Isotopic variations in dissolved inorganic carbon can be pronounced in small lakes, and one consequence is that phytoplankton can have very negative −35 to −45‰ $\delta^{13}C$ values (Oana and Deevey 1960, Deevey *et al.* 1963, Deevey and Stuiver 1964, Rau 1978). Animals feeding on plankton can be distinguished from those feeding on −28‰ terrestrial plant litter that falls into lakes (Rau 1980). Other food sources may also be locally important in freshwater ecosystems. Macrophytic algae in lakes can have ^{13}C-enriched values *vs.* terrestrial materials in some lakes (LaZerte and Szalados 1982). In streams, algae may have $\delta^{13}C$ values either more or less negative than −27‰ C_3 plant litter (Rounick *et al.* 1982, Osmond *et al.* 1981). C_4 plant litter ($\delta^{13}C$ = −13‰) can be an important detrital food source in some subtropical and tropical streams (Parker and Calder 1970).

Lakes and streams offer many possibilities for resolving whether food webs are based on plankton *vs.* terrestrial plant litter. For example, plankton $\delta^{13}C$ varies seasonally by over 15‰ in Lake Kinneret (Stiller 1976, Stiller and Nissenbaum 1980), and plankton feeders should show a similar but delayed variation depending upon trophic level. In contrast, detrital terrestrial materials show no seasonal variations in $\delta^{13}C$ (Stiller 1976), and animals feeding on these materials should have more constant $\delta^{13}C$ values. In streams, consumer $\delta^{13}C$ values may reflect seasonal events such as leaf litter inputs in the fall or spring periphyton blooms.

6. MULTIPLE TRACER STUDIES

6.1. SEDIMENTS AND POC

Carbon isotopic analysis alone often cannot provide definitive answers to questions of origin of carbon in coastal sediments and seston. There are, however, a number of promising approaches which involve a combination of analyses to more accurately "fingerprint" the individual sources of fixed carbon. These include multiple stable isotope tracers with some combination of δD, $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ (*e.g.*, Peters *et al.* 1978, Sweeney and Kaplan 1980, Sweeney *et al.* 1980, Macko 1983); carbon:nitrogen and carbon:hydrogen elemental ratios (*e.g.*, Stuermer *et al.* 1978); analysis of lignin content (*e.g.*, Hedges and Parker 1976); fatty acid analysis (*e.g.*, Schultz and Quinn 1977, Rodier and Khalil 1982); and pyrolysis and subsequent gas-chromatography mass-spectrometry (GC-MS) analysis (*e.g.*, Sigleo *et al.* 1982).

Some of these techniques applied to estuarine seston and sediments have already produced results which suggest that *in situ* phytoplankton production is the most important source of organic carbon. For instance, Sigleo *et al.* (1982) examined the organic composition of colloidal material in the Patuxent River Estuary and in the adjacent open Chesapeake Bay by pyrolysis-GC-MS analysis. No detectable lignin derivatives, indicators of

terrestrial plant material, were found in any of the samples. Phytoplankton were found to be the predominant source of colloidal organic matter in these waters. Such conclusions aid in analyses of isotopic data by simplifying a multi-source model (Fig. 1C) toward a two-source model (Fig. 1A).

6.2. FOOD WEBS

Using more than one chemical tracer can also help resolve complexities of food webs. For instance, multiple $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$, and ^{14}C activity data for animals at deep-sea hydrothermal vents show that these animals differ in many respects from other marine fauna (Rau and Hedges 1979; Rau 1981a,b; Williams *et al.* 1981; Fry *et al.* 1983a), presumably because the hydrothermal vent fauna feeds in a food web based on chemosynthetic bacteria (Jannasch and Wirsen 1979, Cavanaugh *et al.* 1981) rather than on phytoplankton. Use of several isotopes for understanding food webs is becoming more common (Schell 1983, Spies and Des Marais 1983, Schoeninger *et al.* 1983, Mariotti *et al.* 1983, Fry 1984b). Some future applications of stable hydrogen, carbon, nitrogen, and sulfur isotopes are listed in Table 5.

TABLE 5

Possible uses of stable isotopes as food web tracers.

Measurement	Resolves food webs based on:
$\delta^{13}C$	C_3 *vs.* C_4 plants
	Seagrasses *vs.* phytoplankton
	C_3 terrestrial *vs.* marine
	Stream algae *vs.* C_3 or C_4 plants
	Lake plankton *vs.* C_3 plants
$\delta^{34}S$	Benthic *vs.* pelagic producers
	Rooted marsh plants *vs.* phytoplankton
δD	Different algal species
	Fluvial *vs.* oceanic producers (in polar regions)
	Methane oxidizers *vs.* phytoplankton (?)
$\delta^{15}N$	N_2 fixers *vs.* nitrate-using plants
	Marine *vs.* terrestrial food sources

Sulfur in marine algae generally measures +16 to +20‰, close to the +20‰ value of sulfate in seawater (Kaplan *et al.* 1963). On the other hand, rooted estuarine plants (and perhaps benthic microalgae) incorporate, in addition to sulfate, ^{34}S-depleted sulfides into their tissues (Carlson and Forrest 1982); plant $\delta^{34}S$ values as negative as −17‰ have been reported (Fry *et al.* 1982b). In marsh studies where it is important to resolve food web contributions of phytoplankton *vs.* rooted vascular macrophytes (*Spartina, Juncus*), $\delta^{34}S$ values should be useful (Peterson and Howarth 1983). In seas and some lakes where it is desirable to resolve benthic *vs.* pelagic components of food webs, $\delta^{34}S$ measurements should also be helpful.

Animals feeding in a benthic food web should have lower $\delta^{34}S$ values due to incorporation of ^{34}S-depleted sulfides by benthic plants and microbes.

Initial food web studies with stable hydrogen isotopes have shown that animals generally have δD values similar to their diets (except when feeding on *Ulva*) and that δD values can be used to resolve feeding on different species of marine algae (Estep and Dabrowski 1980, Macko *et al.* 1983b). Some controversy exists at present, however, about exchange of hydrogen isotopes between water and organic matter; exchange would complicate a straightforward linkage of δD values to diet (DeNiro and Epstein 1981c). Nonetheless, δD values may prove useful for distinguishing animals feeding in freshwater *vs.* marine food webs in polar areas since δD values of freshwater vs. seawater differ dramatically (Taylor 1974). Anadromous fish and migratory water fowl may exhibit dramatic δD changes as they switch from freshwater to marine diets. Another possible application of δD values lies in distinguishing methane-oxidizing bacteria *vs.* phytoplankton as the basis of some food webs since hydrogen in methane has low δD values, and autotrophic methane-oxidizing bacteria may therefore also have low δD values (Schoell 1982).

Stable nitrogen isotopes may function in offshore systems as trophic indicators because animal $\delta^{15}N$ values increase by $\sim +3‰$ per trophic level (Miyake and Wada 1967, DeNiro and Epstein 1981a). Schoeninger *et al.* (1983) have used $\delta^{15}N$ values to resolve marine *vs.* terrestrial diets and also suggested that low $\delta^{15}N$ values in the Bahamas may indicate marine food webs based on N_2-fixing algae. However, in estuaries where $\delta^{15}N$ differences between potential foods are small and metabolic fractionations by animals and microbes are relatively large (Mariotti *et al.* 1983, Macko and Estep 1983, Estep 1983, Macko *et al.* 1983a), usefulness of $\delta^{15}N$ as a food web tracer may be limited.

7. SUMMARY

Stable carbon isotopic measurements provide useful information about which autotrophs—plants and bacteria—are important sources of carbon in marine and freshwater sediments, POC, and food webs. Transect studies of sediments and POC (section 4) often show clear-cut patterns of isotopic change that can be directly related to the proximity of various carbon sources. This has led to use of simple mixing models (Fig. 1A) in which isotopic data indicate relative importances of plant carbon sources. However, isotopic interpretations of $\delta^{13}C$ data are not always easily made. For instance, while $-27‰$ isotopic values for POC in upper reaches of estuaries may indicate carbon from terrestrial C_3 plants, phytoplankton in these locations may also have $-27‰$ values. Other potential complications discussed in section 4 include isotopic changes during plant decomposition (these appear to be small, $< 2‰$) and also multiple sources of organic matter (Fig. 1C). Uses of several geochemical and isotopic techniques that can

supplement $\delta^{13}C$ data are discussed in section 6.1. Supplemental techniques are needed, especially when sources have similar $\delta^{13}C$ values.

The causes of carbon isotopic variations among autotrophic plants and bacteria are complex (section 3), but $\delta^{13}C$ values encode much potentially interesting information about the pathways and kinetics of autotrophic CO_2 fixation. Ecologists should note that isotopic variations of up to 25‰ have been documented for one aquatic plant (*Potamogeton*) and should be cautious when deciding which plant $\delta^{13}C$ values to use in mixing models.

Isotopic measurements are particularly valuable in food web studies. They provide an independent means of evaluating diet that supplements stomach content analyses. They provide a time-integrated measure of assimilation since analyses are performed on body tissues that are built up from the diet over time. Through analyses of several tissues that have a range of turnover rates, isotopic measurements can be used to identify individual animals that are switching diets. Finally, samples can be fairly simply prepared for isotopic analysis, and commercial firms routinely perform analyses at reasonable rates (currently $30–60 U.S. for one $\delta^{13}C$ analysis).

In food web studies the maxim of "you are what you eat" (*i.e.*, animals have carbon isotopic values similar to their diets) has been extensively tested in laboratory studies (section 5.1), and the maxim is generally valid within about ±2‰ (Fig. 3). Offshore studies of entire natural food webs, however, uniformly indicate a cumulative increase in ^{13}C with increasing trophic level (Fig. 4); an average ^{13}C increase of about 1‰ per trophic level may apply, but there are exceptions (section 5.2). Food web studies in seagrass meadows, salt marshes, and freshwater lakes and streams (sections 5.3 and 5.4) again show that interpretation of $\delta^{13}C$ data is often complex, and a discussion of potential ways to supplement $\delta^{13}C$ food web data with other stable hydrogen, nitrogen, and sulfur isotopic analyses is presented (section 6.2). Since $\delta^{13}C$ and $\delta^{15}N$ values appear to increase by 1 and 3‰, respectively, per trophic level, they are potential indicators of trophic structure in some ecosystems. δD and $\delta^{34}S$ measurements, in contrast, show little change with trophic level (Fry 1981b).

Two major ideas have emerged from the use of stable isotope analyses in estuaries—that photosynthesis by aquatic microorganisms is often the major source of organic carbon for estuarine POC and sediments and that food webs in salt marshes and seagrass meadows are not uniformly based on detrital macrophytes, but on algae in some locations. These ideas challenge some concepts about the importance of vascular plant detritus in coastal ecosystems (Nixon 1980). Sampling along transects and clear definition of end-member isotopic values remain important strategies for testing the importance of a specific carbon source for POC, sediments, or food webs. Isotopic comparisons can reveal major differences in carbon flow between ecosystems and also on much smaller scales (a few meters).

Combined with other isotopic and geochemical techniques, stable carbon isotope analysis can provide definitive answers to questions of the origin of fixed carbon in aquatic ecosystems. Stable isotope analyses generally show

good potential for elucidating trophic relations in freshwater lakes and streams, aquaculture ponds (Schroeder 1983a,b), coral reefs (Land *et al.* 1975, Fry *et al.* 1982a) and kelp beds (Dunton and Schell 1982, Schell 1983). Analyses may also indicate uptake of polluted foods by animals (Rau *et al.* 1981, Spies and DesMarais 1983) or trace migration of marine animals important to man (Killingley 1980; Fry 1981, 1984b; Killingley and Lutcavage 1983). More applications of this versatile tracer technique will undoubtedly appear in the future.

ACKNOWLEDGMENTS

This work was supported by several grants. Grants NASA NGR 15-003-118 and NSF PCM 7910747 to John M. Hayes and Howard Gest, respectively, supported B. Fry; Sapelo Island Research Foundation provided grant support to E. Sherr. Contribution No. 512 of the University of Georgia Marine Institute. We thank the following colleagues for their discussions and criticisms of this paper: John Bauld, John M. Hayes, Stephen A. Macko, Margarita Mangini, Patrick L. Parker, Bruce J. Peterson, Robert Stephenson, and anonymous reviewers.

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Contributions in Marine Science. (1984) Vol. 27:49–63.

^{13}C ENRICHMENT AND OCEANIC FOOD WEB STRUCTURE IN THE NORTHWESTERN GULF OF MEXICO[1]

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ABSTRACT

The use of $\delta^{13}C$ measurements to indicate trophic levels of offshore animals was tested by analyzing four components of food webs in the northwestern Gulf of Mexico. A progression of increasing ^{13}C contents (less negative $\delta^{13}C$ values) occurred from particulate organic carbon ($\bar{x}$ = −21.7‰) to zooplankton ($\bar{x}$ = −20.2) to benthic crustacean gut contents ($\bar{x}$ = −17.8‰) to whole benthic crustaceans ($\bar{x}$ = −16.9‰), so that the degree of ^{13}C enrichment functioned as a crude indicator of trophic level. Six transects made off Texas and Louisiana from near shore to approximately 160 m during 1979 and 1980 showed that considerable seasonal and spatial variation occurred in this average pattern of ^{13}C enrichment, and that this variation was not linked to inputs of terrestrial carbon. Benthic crustaceans collected in the same trawl had very similar $\delta^{13}C$ values (within 1.3‰), regardless of species. Shipboard experiments showed that assimilation could account for the observed 0.9‰ ^{13}C enrichment in these animals *vs.* their diets. Previous findings of a 0.35‰ increase in ^{13}C of offshore plankton per °C increase in temperature (Fontugne and DuPlessy 1981) were not confirmed in this study. While considerable isotopic variation occurs offshore and complicates simple assessment of trophic level from ^{13}C enrichment data, reduced isotopic variation appears useful for identifying consumers at higher trophic levels.

Accepted 9 March 1984

INTRODUCTION

Stable H, C, N, and S isotope measurements have been widely used to study the dietary relationships between animals and their foods (*e.g.*, Estep

and Dabrowski 1980; Minson, Ludlow, and Troughton 1975; DeNiro and Epstein 1981; Mekhtiyeva, Pankina, and Gavrilov 1976). These chemical analyses complement traditional visual means of studying diets and have proven particularly useful when applied to problems such as the assimilation of detrital or dissolved foods (Hackney and Haines 1980; Rau and Anderson 1981) or diets of prehistoric peoples (van der Merwe 1982). A basic premise in these studies is that animals bear a fixed isotopic relationship to their foods. In the absence of metabolic fractionations, animals should have precisely the same isotopic composition as their foods. However, metabolic fractionations do occur, with the consequence that especially top carnivores may have an isotopic composition substantially different from that of the plants upon which they ultimately depend (Miyake and Wada 1967; McConnaughey and McRoy 1979; Rau, Mearns, Young, Olson, Schafer, and Kaplan 1983).

For carbon, the evidence for cumulative food web fractionations comes primarily from investigations of oceanic ecosystems. Marine animals are commonly enriched in ^{13}C (have less negative $\delta^{13}C$ values) relative to oceanic particulate matter (Williams and Gordon 1970; Eadie 1972; Gormly and Sackett 1977; Thayer, Govoni, and Connally 1983), with benthic invertebrates such as shrimp showing the largest enrichments (Fry and Parker 1979; Rodelli 1981; Fry, Scalan, and Parker 1983). McConnaughey and McRoy (1979) have used such ^{13}C enrichments to make initial estimates of food web structure in the Bering Sea.

To investigate trophic structure in the offshore Gulf of Mexico using $\delta^{13}C$ analyses, we collected samples of particulate organic carbon (POC), zooplankton, benthic crustaceans, and stomach contents of benthic crustaceans during two years along six offshore transects. We use the data to evaluate 1) possible ^{13}C inputs from land to the offshore food web, 2) a suggested dependence of zooplankton $\delta^{13}C$ on temperature (Sackett, Eckelmann, Bender, and Bé 1965; Fontugne and Duplessy 1981), 3) variability in the degree of ^{13}C enrichment occurring per trophic level, and 4) the causes of the ^{13}C enrichments that occur offshore.

METHODS

Benthic crustaceans were collected with a 10.7 m wide, 12.6 mm mesh otter trawl along several transects in the northwestern Gulf of Mexico (Fig. 1). Benthic crustaceans were either immediately dissected and frozen for later use, or, for assimilation experiments, kept alive for 1–2 hours in salt water tanks so that fecal materials could be collected. Zooplankton samples were collected in oblique tows from the bottom to the surface with a 250 μ-mesh net. For POC, 1–17 l of seawater were filtered onto precombusted (4 hours, 450°C) glass-fiber filters (Gelman GF/C; pore size 1.2 μ) which were then frozen. Salinity and temperature were each measured to ± 0.01 units (‰ or °C, respectively) using an Oceanography International model RW5-3 salinometer mounted shipboard in a flow-through chamber during 1980 cruises; for measurements made off Barataria Bay in 1979, a refractometer precise to ± 1‰ salinity units and a thermometer accurate to ± 0.1°C were used.

Most benthic shrimp and stomatopods were identified using the key of Wood (1974); some rarer specimens were identified by reference to collections kept at the Port Aransas Marine

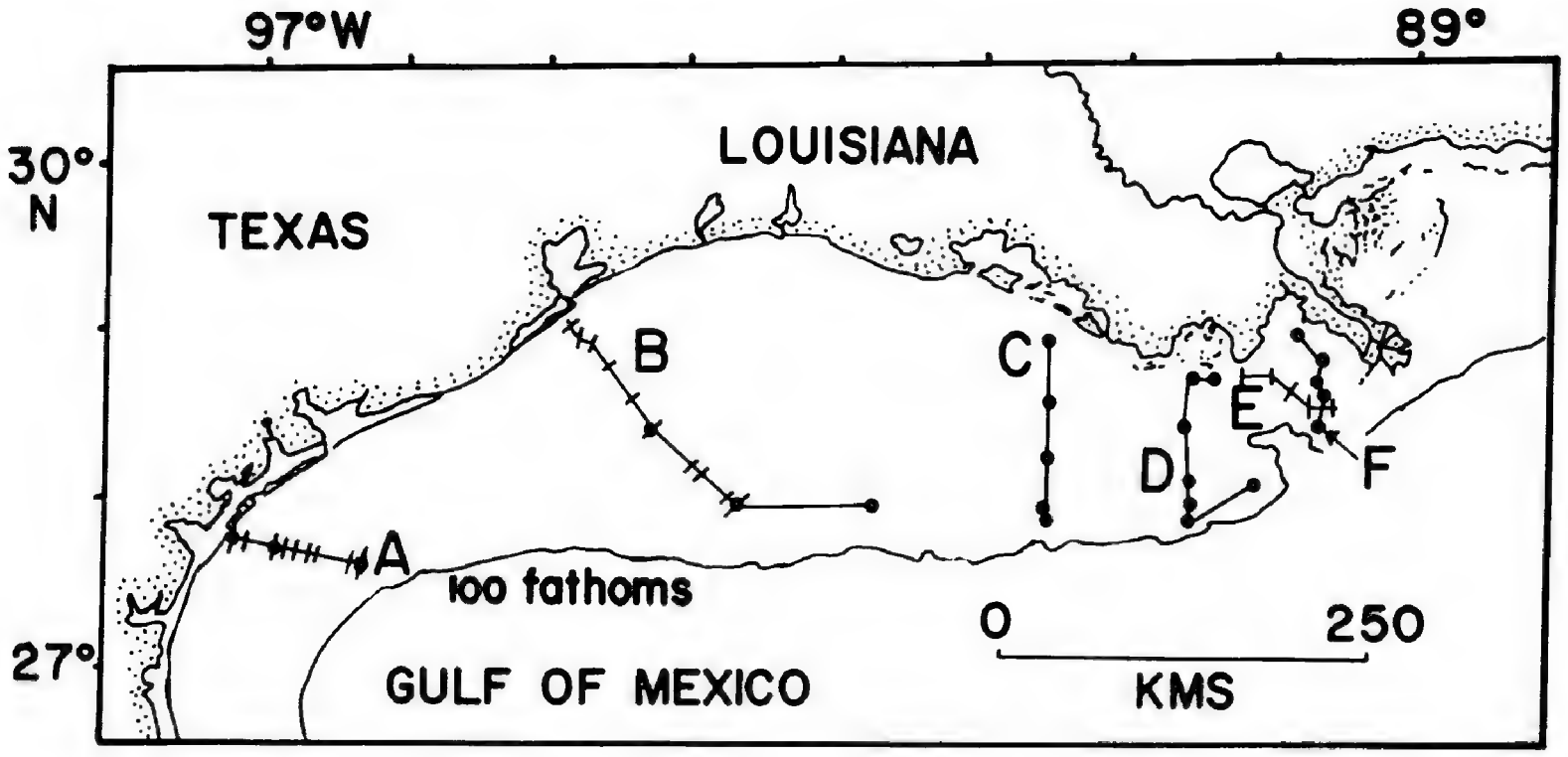

FIG. 1. Offshore sampling transects, 1979–80. Bars and dots denote station locations for samples collected in October, 1979 (o), May, 1980 (–), and October, 1980 (•). Transects are located opposite the following major bays: Corpus Christi Bay (A), Galveston Bay (B), Atchafalaya Bay (C), Terrebonne Bay (D), and Barataria Bay (E and F).

Laboratory. Benthic crustaceans were sorted into groups by species and tail muscle tissue was taken from 5–25 individuals, pooled, then dried at 60°C for later isotopic analysis. POC and zooplankton samples were briefly acidified with 1N HCl to remove carbonates, rinsed and dried (October, 1979 and May, 1980 samples) or acidified, then dried without rinsing (October, 1980 samples). Proventriculi (foreguts) were removed from benthic crustaceans aboard ship and frozen. In the laboratory, foregut contents were removed and contaminating pieces of flesh or foregut removed with foreceps under a dissecting microscope. Hindgut and fecal samples were extruded from their surrounding membranous sheaths aboard ship and frozen. To insure complete removal of carbonates present in mollusc shells, foregut, hindgut, and fecal samples were treated overnight with strong acid (6 N HCl), then filtered and rinsed with distilled water prior to isotopic analysis.

Samples of 2–10 mg were mixed with CuO and sealed in evacuated Pyrex tubes that had previously had one end drawn out to a point; combustions were performed in a muffle furnace for 30 minutes at 590°C (Sofer 1980). Combustion appeared complete, as black carbon residues indicative of incomplete combustion (Boutton, Wong, Hachey, Lee, Cabrera and Klein 1983) did not form on inside walls of the Pyrex tubes. To collect the resulting CO_2, sealed tubes were inserted into rubber tubing attached to an evacuated glass line, the glass tips were snapped off, and diffusing CO_2 was collected for 4 minutes in a glass U trap cooled by liquid nitrogen. Noncondensible gases were then pumped away and purified CO_2 obtained after replacing the liquid nitrogen with a dry ice/acetone mixture. Percent total organic carbon (TOC) was determined with a calibrated mercury manometer to measure CO_2 yields.

The isotopic composition of the gas was measured in an isotope ratio mass spectrometer (Micromass 602E). All results are expressed in $\delta^{13}C$ notation relative to the international PDB standard (Craig 1957), where

$$\delta^{13}C = [(R_{sample}/R_{standard}) - 1] \times 10^3 \text{ and}$$
$$R = {}^{13}C/{}^{12}C.$$

Analytical precision was evaluated in several ways. 1) Aliquots of a large sample of shrimp muscle tissue were combusted in three ways—in Pyrex sealed tubes, in quartz sealed tubes at

900°C, and in a "Craig-type" recirculating system (Craig 1953) with subsequent removal of sulfur and nitrogen oxides using 400°C copper. Mean values for these methods agreed within 0.1‰. The Pyrex sealed tube method gave a standard deviation of 0.19‰ for 46 replicate combustions (range = 0.75 for 45 samples; total range for 46 samples = 1.0‰). 2) Paired comparisons for 56 offshore shrimp and stomatopod samples were made by the Pyrex sealed tube method and the LECO induction furnace method of high temperature (> 1500°C) combustion (Parker, Behrens, Calder and Schultz 1972). Results were usually similar within 0.2‰ for the two methods, with a mean difference of 0.05‰. 3) Paired comparisons were also made for selected POC and zooplankton samples in sealed quartz (900°C) and Pyrex (590°C) tubes. Isotopic values were usually similar within 0.2‰. In sum, we estimate that overall analytical error was generally less than ± 0.3‰ for individual determinations.

RESULTS

$\delta^{13}C$ UNIFORMITY AMONG BENTHIC CRUSTACEANS

The nine shrimp and three stomatopod species frequently collected in benthic trawls are listed in Table 1. When collected in the same trawl, these benthic species had essentially identical $\delta^{13}C$ values. Because of significant seasonal and spatial variations in $\delta^{13}C$ values of benthic crustaceans, data were normalized on a per trawl basis prior to testing for any small, but possibly significant isotopic differences among species. This normalization was accomplished by designating two species as references, then subtracting one of their isotopic values from values of other benthic crustaceans collected in the same trawl. The two reference species were *Squilla empusa* (shallow-water) and *Solenocera vioscai* (deep-water). Isotopic values of these two reference species were similar for five trawls in which they occurred together (mean difference ± S.D. = 0.04 ± 0.6‰). Normalized data were thus in the form of paired comparisons to reference species. In no case were these differences significant ($P > 0.05$, paired t-test) and overall mean differences between species did not exceed 1.3‰ (Table 1). (Other methods of normalizing the data, based on using the average of species collected at several adjacent stations as the normalizing value, gave the same result of no significant differences among species.) For further graphical and statistical purposes, these species are therefore not considered separately and appear together as "benthic crustaceans."

TRANSECTS AND ^{13}C ENRICHMENT

Transects made from shoreline to 100–160 m depths showed few cross-shelf isotopic trends in $\delta^{13}C$ values for POC, zooplankton (ZPL) or benthic crustaceans (Figs. 2 and 3). The most pronounced cross-shelf variations tended to occur in the samples collected near shore (Figs. 2A, 2B, and 3A). Isotopic influences from rivers and estuaries thus appeared confined to near-shore regions.

A regular pattern of ^{13}C enrichment occurred in each transect. $\delta^{13}C$ values were most negative for POC, intermediate for zooplankton, and least negative for benthic crustaceans (Table 2). Mean $\delta^{13}C$ values were significantly different ($P < 0.05$, GT-2 test, Sokal and Rohlf 1981) for POC, zoo-

TABLE 1

Isotopic similarities among shrimp and stomatopod muscle tissues.

Species	Mean $\Delta\delta^{13}C$ *	S.D.	N
Parapandalus longicauda	+0.3	0.17	3
Sicyonia dorsalis	+0.01	0.45	19
Trachypenaeus similis	0.00	0.49	20
Squilla empusa †	0.00	----	--
Solenocera vioscai	0.00	----	--
Sicyonia brevirostis	-0.09	0.39	9
Squilla chydaea †	-0.11	0.39	11
Xiphopenaeus kroyeri	-0.3	0.28	2
Parapenaeus longirostris	-0.38	0.52	6
Squilla edentata †	-0.8	----	1
Sicyonia stimpsoni	-0.8	----	1
Processa sp.	-1.0	----	1

* $\Delta\delta^{13}C$ = difference in $\delta^{13}C$ relative to *Squilla empusa* or *Solenocera vioscai* collected in the same trawl.

† Stomatopod (others are shrimp species.)

plankton, and benthic crustaceans for seven of the eight transects; the exception is that POC and zooplankton means did not significantly differ in the October, 1980 collections along the Barataria transect (Table 2). Averaged over all eight transects, mean $\delta^{13}C$ enrichments relative to POC were +1.9‰ for zooplankton and +5.6‰ for benthic crustaceans (Table 2).

While these overall patterns of ^{13}C enrichment were fairly consistent, isotopic values in the offshore Gulf varied with season and location. Seasonal variations were evident off the Texas coast in 1980. POC collected off Galveston, and zooplankton and benthic crustaceans collected at < 35 m off both Galveston and Corpus Christi during May had significantly ($P < 0.05$) more negative average $\delta^{13}C$ values than comparable October samples (Table 2). Significant spatial variations also occurred. Along a gradient from south Texas towards the Mississippi River, a progression toward ^{13}C enrichment or less negative $\delta^{13}C$ values was observed (October 1980 transects, Corpus Christi to Barataria, Table 2). Benthic crustaceans collected offshore of 35 m and POC had $\delta^{13}C$ values significantly less negative in the Barataria and Terrebonne transects than in the Corpus Christi transect ($P < 0.001$, GT-2 test). $\delta^{13}C$ values of zooplankton showed a parallel trend towards less negative values towards the Mississippi, but differences

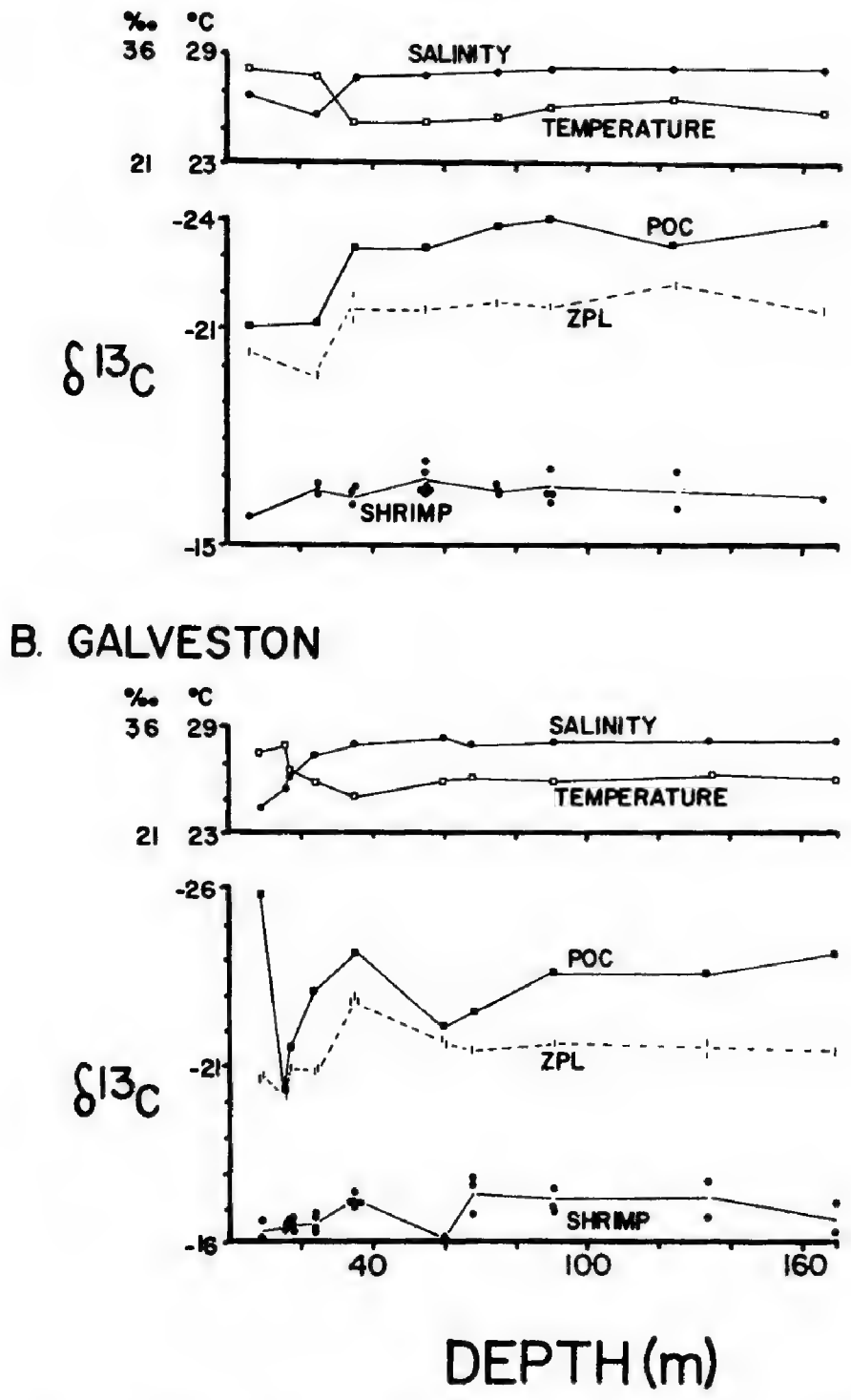

FIG. 2. Temperature, salinity, and $\delta^{13}C$ data collected off Texas, May, 1980 (transects A and B, Figure 1). POC = particulate organic carbon, ZPL = zooplankton.

between means were not significant ($P > 0.05$, GT-2 test). Other examples of spatial variations occurred. Benthic crustaceans collected inshore of 35 m along the Corpus Christi and Galveston transects in October, 1980 averaged significantly less negative ($P < 0.05$, t test) than benthic crustaceans collected farther offshore (Table 2). In all, these seasonal and spatial variations were greater for POC and zooplankton than for benthic crustaceans as mean values showed a 3.7‰ range for POC, 2.3‰ for zooplankton, and 1.9‰ for benthic crustaceans (Table 2). This reduction in isotopic variation as one moves up the food chain might well be expected.

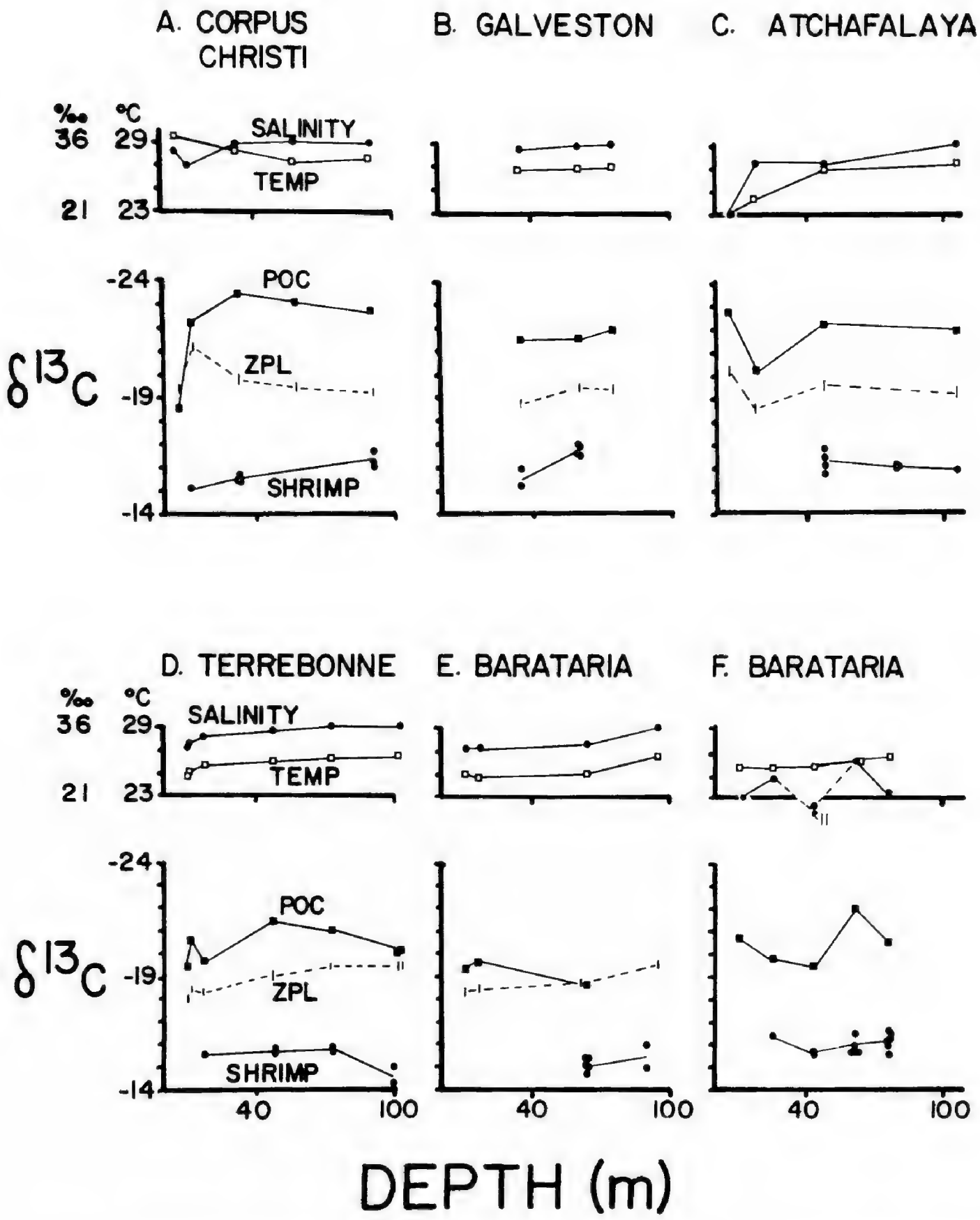

FIG. 3. Temperature, salinity, and $\delta^{13}C$ data collected off Texas and Louisiana, October, 1980 (panels A–E), and October, 1979 (panel F). POC = particulate organic carbon, ZPL = zooplankton. Transect locations are given in Figure 1.

ZOOPLANKTON CORRELATIONS WITH POC, °C, AND SALINITY

Planktonic $\delta^{13}C$ data showed consistent relationships to temperature, salinity, and $\delta^{13}C$ values of POC, but these relationships differed between cruises (Figs. 4 and 5). These between-cruise differences were most striking

TABLE 2

Mean $\delta^{13}C$ values ± S.D. (n) by transect for POC, zooplankton, and benthic crustaceans, plus (in brackets) ^{13}C enrichments relative to POC.

Transect	POC	Zooplankton	Benthic Crustaceans	
			Inshore (< 35 m)	Offshore (> 35 m)
A. May, 1980--Texas				
Corpus Christi	-22.9 [0] ± 1.2 (8)	-21.3 [+1.6] ± 0.8 (8)	-16.3 [+6.6] ± 0.5 (3)	-16.6 [+6.3] ± 0.3 (19)
Galveston	-23.0 [0] ± 1.6 (10)	-21.3 [+1.7] ± 0.7 (10)	-16.5 [+6.5] ± 0.2 (12)	-17.1 [+5.9] ± 0.5 (15)
B. October, 1980-- Texas and Louisiana				
Corpus Christi	-22.9[a] [0] ± 0.6 (4)	-19.8 [+3.1] ± 0.8 (5)	-15.3 [+7.6] ± 0.3 (5)	-16.3 [+6.6] ± 0.4 (3)
Galveston	-21.7 [0] ± 0.2 (3)	-19.2 [+2.5] ± 0.4 (3)	-15.6 [+6.1] ± 0.5 (2)	-16.8 [+4.9] ± 0.2 (4)
Atchafalaya	-21.8 [0] ± 1.1 (4)	-19.4 [+2.4] ± 0.7 (4)	---	-16.1 [+5.7] ± 0.4 (8)
Terrebonne	-20.4 [0] ± 0.7 (7)	-19.0 [+1.4] ± 0.6 (7)	-15.6 [+4.8] (1)	-15.4 [+5.0] ± 0.6 (6)
Barataria	-19.3 [0] ± 0.5 (3)	-18.8 [+0.5] ± 0.5 (4)	---	-15.2 [+4.1] ± 0.4 (7)
C. October, 1979-- Louisiana				
Barataria	-20.6 [0] ± 1.0 (5)	---	-16.4 [+4.2] (1)	-16.0 [+4.6] ± 0.4 (14)
Mean ^{13}C Enrichment	0	+1.8	+5.9	+5.5

[a]Sample nearest shore not included.

in the case of temperature as May collections showed a trend toward less negative $\delta^{13}C$ values with increasing temperature, while October samples showed an opposite trend (Fig. 4). October samples also clearly did not conform to correlations established by Fontugne and Duplessy (1981) for plankton $\delta^{13}C$ vs. temperature (Fig. 4, dotted lines).

CAUSES OF BENTHIC ^{13}C ENRICHMENT

The isotopic relationship between benthic crustaceans and their foods was investigated by collecting 74 foregut (proventriculus) samples at most stations shown in Figure 1 during 1979–80. Foregut samples averaged 2.8‰ more negative than muscle tissue in animals from which they were collected.

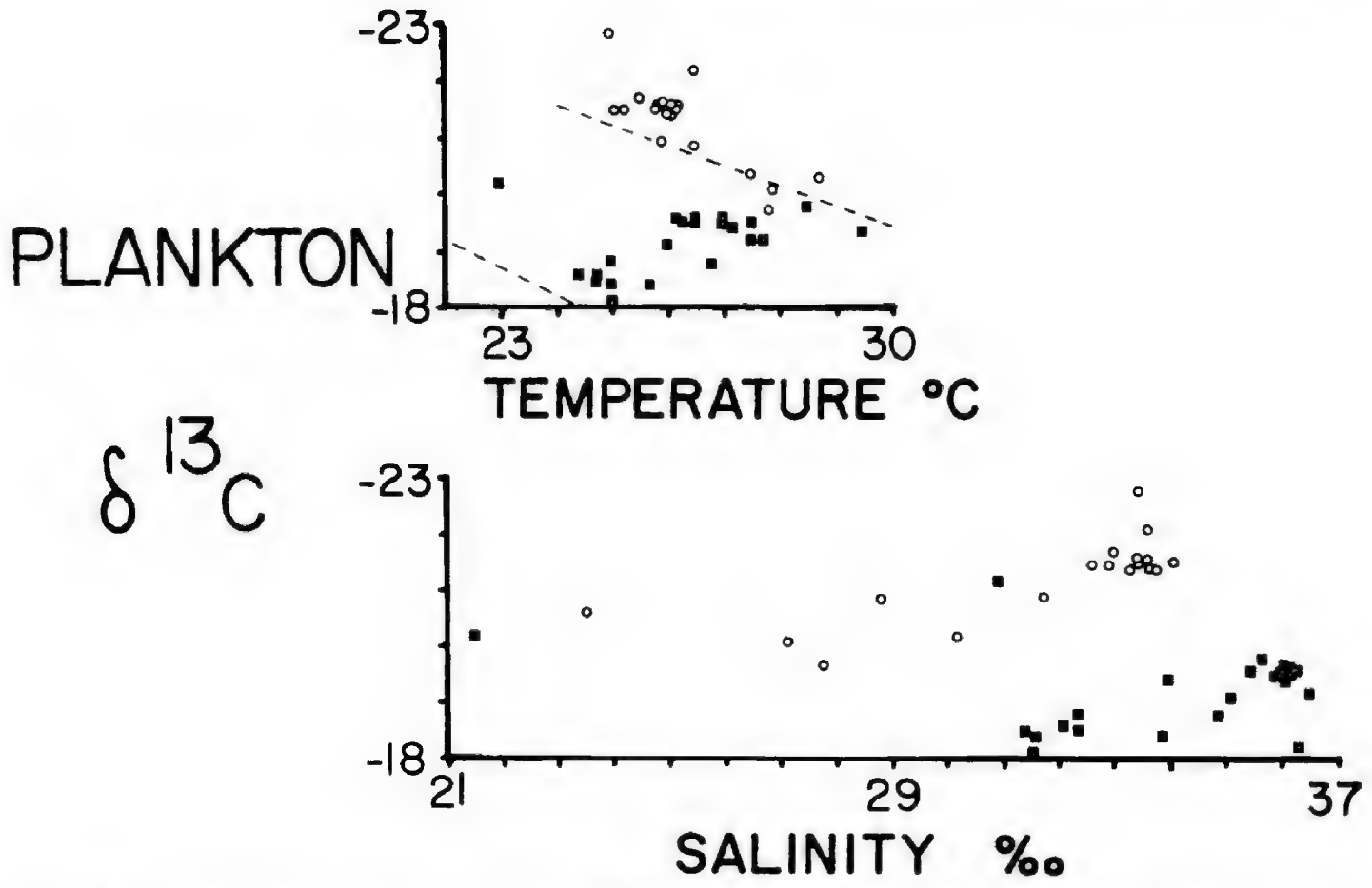

FIG. 4. Relationship of zooplankton $\delta^{13}C$ to temperature and salinity. Dotted lines in upper panel indicate zooplankton $\delta^{13}C$/temperature relationships established by Fontugne and DuPlessy (1981) for temperatures > 25°C (right line) and < 25°C (left line). Open circles denote May samples, closed squares October samples.

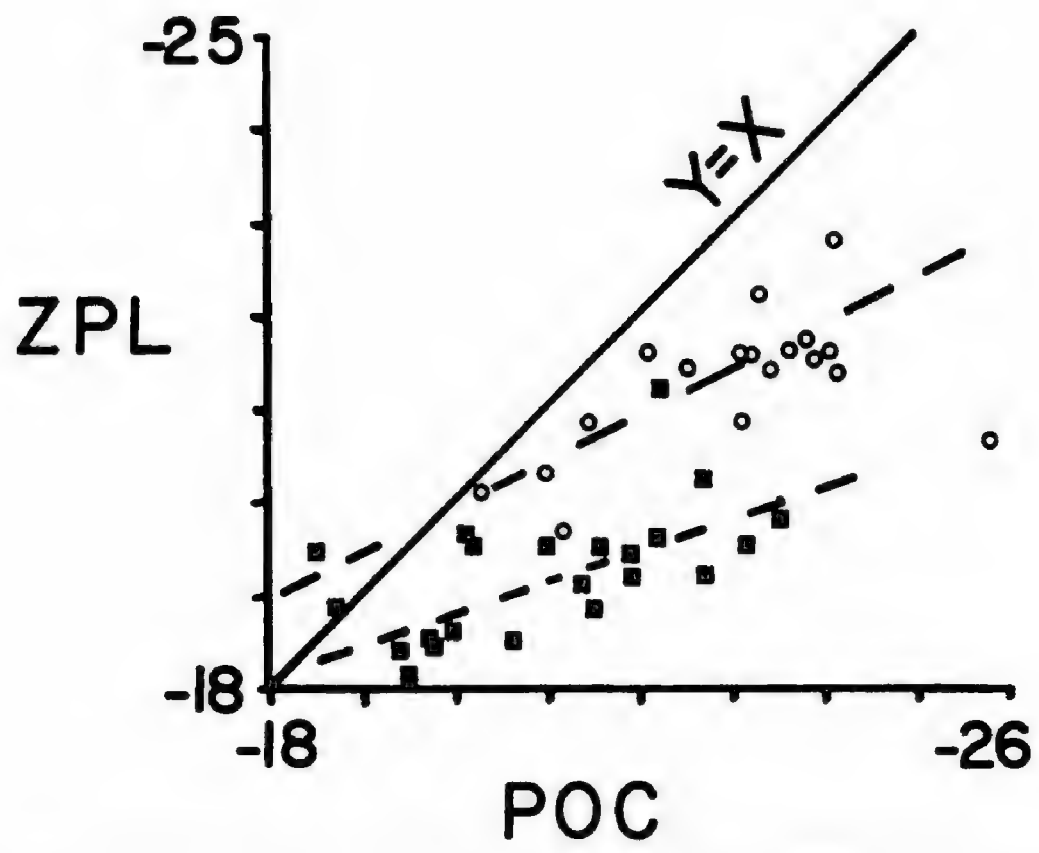

FIG. 5. Isotopic relation between particulate organic carbon (POC) and zooplankton. Dotted lines are best-fit trend lines through most May (open circles) and October (closed squares) data.

Field and laboratory control experiments (Fry 1981b) showed that digestive secretions do not significantly alter the isotopic composition of foods dissected from stomachs. However, the strong acid plus rinsing pretreatment used in this study did alter the isotopic composition of foods, resulting in $\delta^{13}C$ values that averaged 1.1‰ more negative than acid-treated foods that were not rinsed, but evaporated to dryness (S.D. = 1.0, N = 6; Fry 1981b). After adding a compensatory +1.1‰ factor to the gut content values, these corrected values still averaged 1.7‰ more negative than muscle tissue (Fig. 6).

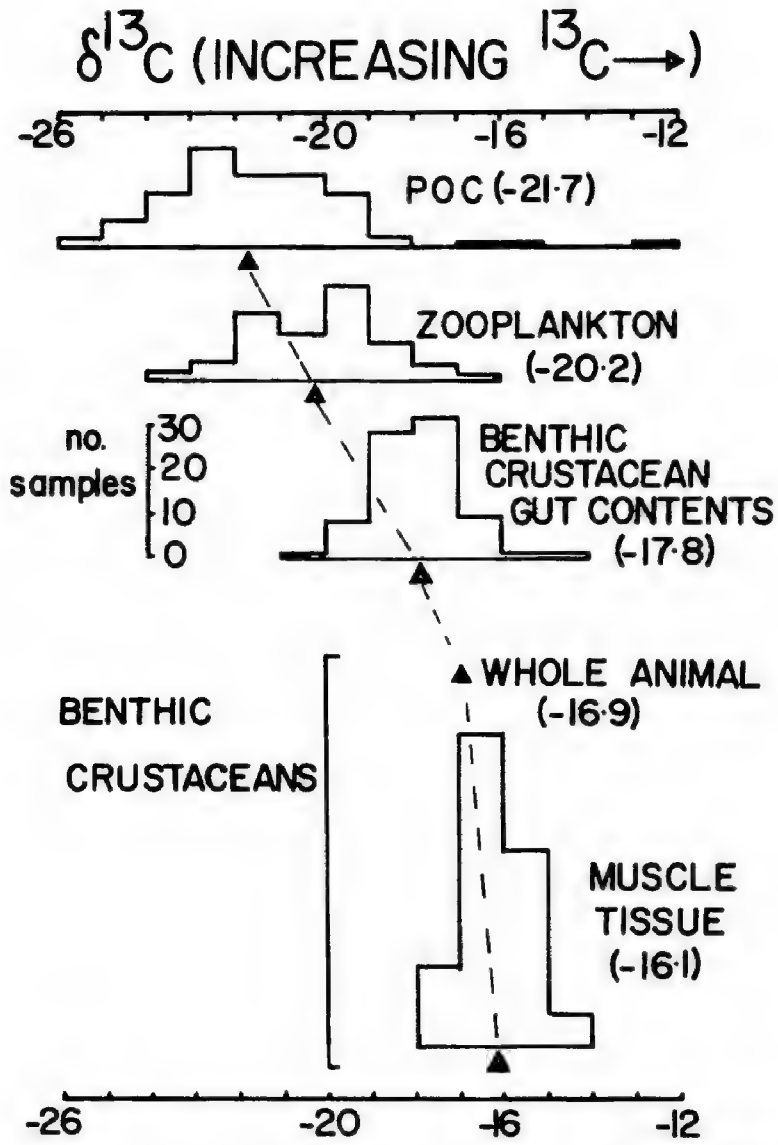

FIG. 6. Histogram of $\delta^{13}C$ values in the Gulf of Mexico. Triangles and numbers in parentheses indicate mean values. Dotted line connecting mean values indicates increasing ^{13}C enrichment with trophic level. Sources for this figure include: Sackett and Thompson 1963, Calder 1969, Eadie and Jeffry 1973, Gormly and Sackett 1977, Eadie *et al.* 1978, Fry and Parker, 1979, this study.

A small difference was found between muscle tissue *vs.* whole animal carbon. Comparisons for three individual benthic crustaceans showed that muscle was enriched in ^{13}C by 0.5, 0.9, and 1.1‰ ($\bar{x}$ = 0.8‰) relative to whole animal carbon. Combining the 1.1 and 0.8‰ correction factors, we obtain the result that whole benthic crustaceans showed a net 0.9‰ enrichment in ^{13}C relative to $\delta^{13}C$ values of their foods (Fig. 6).

The causes of this 0.9‰ ^{13}C enrichment were investigated in six shipboard experiments. Groups of 25–50 benthic shrimp were held in tanks for 1–2 hours immediately after being collected in trawls so that feces could be collected. Pooled foregut and midgut samples were obtained from a second group of 25–50 shrimp taken from the same trawl. Comparisons of foregut, midgut and fecal samples showed systematic isotopic differences. Midgut and fecal samples were always depleted in ^{13}C relative to foregut samples (Table 3). The mean organic content of these samples, measured manometrically as % TOC, also declined from 19 to 9% between foregut and feces (Table 3). By comparing both the isotopic and organic carbon changes between samples of foregut and fecal materials, the isotopic value of assimilated materials could be calculated; it averaged +1.3‰ relative to foods found in the foregut (Table 3). While these results are primarily based on samples that had been rinsed after strong acid treatment, experiment 6, in which samples were evaporated to dryness rather than rinsed, showed a similar ^{13}C enrichment (Table 3). These experiments show that the mean +1.3‰ ^{13}C enrichment occurring during assimilation could account for the mean +0.9‰ difference found between whole benthic crustaceans and their foods.

TABLE 3

Net ^{13}C enrichment during assimilation and excretion by benthic shrimp.

Experiment	Proventriculus		Midgut		Feces		Assimilated*		^{13}C Enrichment
	$\delta^{13}C$ (A)	%TOC	$\delta^{13}C$	%TOC	$\delta^{13}C$	%TOC	$\delta^{13}C$ (B)	A.E.	(B-A)
1	-18.6	20.6	-20.0	11.3	-19.7	4.9	-18.4	80	+0.2
2	-18.7	21.2	-19.2	19.7	-19.3	13.3	-18.0	43	+0.7
3	-17.7	17.2	---	---	-18.9	11.8	-15.3	36	+2.4
4	-18.7	15.8	-19.2	13.3	-20.6	9.5	-16.3	44	+2.4
5	-18.2	27.7	-18.7	12.4	-19.1	11.8	-17.8	69	+0.4
6**	-18.0	9.5	-18.9	7.9	-20.1	4.7	-16.3	53	+1.7
Mean (S.D.)	-18.3 (0.4)	18.7 (6.1)	-19.2 (0.5)	12.9 (4.3)	-19.6 (0.6)	9.3 (3.7)	-17.0 (1.2)	54 (17)	+1.3 (1.0)

*The values for $\delta^{13}C$ of carbon assimilated and assimilation efficiency (A.E.) were derived from differences between food (proventriculus contents) and feces. A.E. = U' = [(F' - E')/(1 - E')(F')] x 100 where F' = %TOC in the proventriculus and E' = %TOC in the feces (Condrey et al., 1972). Further, $\delta^{13}C_{assimilated} = [(\delta_{proventriculus} - \delta_{feces})/A.E.] + \delta_{feces}$.

**Samples in this experiment were not rinsed after acidification; samples were rinsed after acidification in the other five experiments.

DISCUSSION

This study suggests a more refined way of using $\delta^{13}C$ data to deduce oceanic trophic structure. Samples collected in cross-shelf transects showed that ^{13}C enrichments are regularly observed in deeper water biota that are

presumably well-isolated from land and river run-off (Figs. 2 and 3). This confirms reports of ^{13}C enrichments made in studies where samples were collected in a much less systematic manner (Williams and Gordon 1970, Eadie 1972, Gormly and Sackett 1977, Fry and Parker 1979, McConnaughey and McRoy 1979, Rodelli 1981, Fry *et al.* 1983). However, ^{13}C enrichments were not constant over time and space (Table 2; Fig. 5), so that the degree of ^{13}C enrichment can function only as a crude indicator of trophic position. Both the degree and timing of isotopic variation should be useful additional indicators of trophic position. Isotopic variation was greatest for POC, intermediate for zooplankton, and smallest for benthic crustaceans (Table 2; Fig. 6), as expected if higher level consumers integrate variations occurring at lower trophic levels. By this reasoning, a continuum should exist with small lower level consumers displaying the largest $\delta^{13}C$ variations and large top carnivores displaying very little $\delta^{13}C$ variation. When phytoplankton vary in their $\delta^{13}C$ values, the timing of ensuing isotopic changes in consumers could be an important indicator of trophic position. As phytoplankton $\delta^{13}C$ values change, herbivore isotopic values should most quickly reflect this change, while changes in top carnivores may be much delayed. Such lag effects may account in part for the variable isotopic enrichment observed between zooplankton and their particulate foods (Fig. 5).

Central to using isotopic variation as an indicator of trophic position is establishing how much isotopic variation occurs in offshore ecosystems. This study provides preliminary estimates of variability in offshore POC and biota. The +1‰ shift found in inshore benthic crustacean $\delta^{13}C$ data from May to October (Table 2) may be a consistent feature in the offshore Gulf; a similar +1.2‰ shift was also observed in benthic crustaceans from July to October in 1978 (Fry 1981a). Variations in POC and zooplankton $\delta^{13}C$ values may be more rapid and need more intensive sampling to establish long-term trends. One indication of rapid change comes from comparing our October results for the area off Barataria Bay with December and February results reported for this same area in 1979–80 by Thayer *et al.* (1983). Comparisons of mean values for October *vs.* (December + February) collections in this area give −20.0 *vs.* −23.2‰ for total POC, and −18.9 *vs.* −21.8‰ for total zooplankton (Table 2; Thayer *et al.* 1983, Table 2).

McConnaughey and McRoy (1979) assumed that a preferential loss of $^{12}CO_2$ during respiration causes the ^{13}C enrichment observed in oceanic food webs. This assumption is based on three of four experiments with terrestrial animals in which respired CO_2 was enriched in ^{12}C by < 1‰ relative to the diets (DeNiro and Epstein 1978). Data collected for marine benthic crustaceans in this study show that net ^{12}C losses occurring in assimilation and excretion can also account for offshore ^{13}C enrichments (Table 3). This net effect could reflect a higher assimilation efficiency for proteins than for other components of the diet (Condrey, Gosselink and Bennett 1972), as amino acid fractions have been shown to be about 3‰ enriched in ^{13}C relative to whole POC or plankton foods (Degens, Behrendt, Gotthardt and Reppmann 1968; Eadie, Jeffrey and Sackett 1978).

Fontugne and Duplessy (1981) have suggested that $\delta^{13}C$ values of marine

plants and plankton are dependent on temperature and become 0.35‰ less negative per °C increase. Data collected during this study did not support this view (Fig. 4), but rather the conclusions of other studies that plankton $\delta^{13}C$ values are dependent on water mass or variations in the species composition of phytoplankton communities (Sackett, Eadie and Exner 1974; Fontugne and Duplessy 1978; Wong and Sackett 1978; Rau, Sweeney and Kaplan 1982). The detailed reasons for plankton $\delta^{13}C$ variations observed in the field have yet to be established.

In sum, $\delta^{13}C$ studies show some promise for elucidating general trophic structure in oceans. Seasonal studies of systems in which phytoplankton $\delta^{13}C$ varies should prove useful in determining trophic level on the basis of both mean ^{13}C enrichment and $\delta^{13}C$ variation over time. In some cases, the variation in $\delta^{13}C$ may be more informative than the degree of ^{13}C enrichment as the degree of ^{13}C enrichment can vary with the isotopic composition of the food source (Fig. 5, DeNiro and Epstein 1978, Fry and Arnold 1982). The widespread isotopic variation documented in this study needs to be carefully considered before using $\delta^{13}C$ data to estimate the trophic positions of offshore animals.

ACKNOWLEDGMENTS

We thank the crew of the *R.V. Longhorn* for their assistance in sampling. This research was supported by NSF grant 77-27009 to P. L. Parker. Nancy Rabalais and Scott Holt provided assistance with collection and taxonomy. Contribution #618 from the Marine Science Institute at Port Aransas.

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PHYTOPLANKTON PRODUCTION IN THE CORPUS CHRISTI BAY ESTUARY[1]

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ABSTRACT

The Texas Gulf coast is characterized by a number of subtropical estuaries which have great economic and ecologic value in that they support important regional fisheries through production of new organic matter by phytoplankton photosynthesis. One of these estuaries, the Corpus Christi Bay ecosystem, was studied for a three-year period to define temporal and spatial variability in its primary production and to elucidate environmental factors important in regulating production. Mean annual phytoplankton production at the various sampling sites increased with distance from the riverine influence of the estuary. This pattern was most closely associated with deeper, less-turbid waters at the oceanic end of the estuary that provided a greater euphotic zone. Variability in measured primary productivity rates between sites was most influenced by water column nutrients in January and July and more significantly correlated to salinity changes in April and October. From the three years of data, annual phytoplankton production was estimated to be 174.1 g $C/m^2/yr$, which represented 52% of total new organic production in this estuary. In contrast, macrophytes and tidal flat algae comprised the remainder of new organic carbon production. Annual production was found to be most significantly affected by freshwater input from either river flow or rainfall, depending upon where production measurements were made in the estuary. High turbidity of this estuarine ecosystem was thought to limit production in contrast to other north American estuaries. It was concluded from the study results that long-term maintenance of primary production in this estuary is accomplished through nutrient recycling while acute changes from both meteorologic and hydrologic forcing cause short-term increases in production that sustain steady-state and replenish lost materials to the system.

Accepted 13 April 1984

INTRODUCTION

The Texas coast of the Gulf of Mexico is characterized by a number of large estuarine lagoon systems lying behind a series of coastal barrier beach islands. These estuaries have great economic and ecological value in that

they support valuable fisheries of the northwestern Gulf (Gunter 1967). The production of new organic matter by phytoplankton through photosynthesis is a basic process of these estuarine ecosystems which provides the food resources for higher trophic levels, including the species harvested by man. Bahr, Day and Stone (1982) have demonstrated a quantitative relationship between secondary production of aquatic consumers in the coastal zone of the Gulf and estuarine primary production. Gilmartin and Revelante (1978) have also suggested that phytoplankton processes in estuarine lagoons may even influence ecosystem dynamics of inshore continental shelf waters. Measurements of the rate of new organic matter production by phytoplankton in coastal estuaries are therefore of practical concern as a principle indicator of the richness and health of these ecosystems.

The physical and chemical environment of an estuarine system can strongly influence the primary productivity rates of phytoplankton communities. In most estuarine communities, light and the availability of nitrogen have been shown to be the primary external factors which regulate phytoplankton production (Ryther and Dunstan 1971, MacIsaac and Dugdale 1972). For Texas estuaries, superimposed upon light and nutrient regulation of phytoplankton production are synergistic effects related to the wide variations observed in salinity. Texas estuaries span a rainfall spectrum that produces a salinity gradient from nearly fresh at the Louisiana border to extremely hypersaline at the Mexican border.

General information is available concerning gross primary productivity of several of the major estuarine systems along the Texas coast (*e.g.* Odum and Wilson 1962; Odum 1963; Odum, Cuzon de Rest, Beyers and Allbaugh 1963; Odum 1967; Flint, Rabalais and Kalke 1982). Some of this data has been tabulated as measures of oxygen produced per unit area or standing crop of chlorophyll *a*. All the information, however, only sparsely covers any of the major Texas estuaries and none accounts for temporal variability that can occur in these systems and that is related to extreme salinity fluctuations. Therefore, the objective of this study was to define the spatial and temporal variability in phytoplankton primary production in one of the major Texas estuaries, the Corpus Christi Bay estuary. Besides defining variability it was hoped that these investigations would elucidate some of the factors important in regulating productivity rates in this estuary.

STUDY AREA

The Corpus Christi Bay estuary is one of seven major estuarine ecosystems along the Texas coast and represents a total open-water surface area of 432.9 km^2. This estuary is shallow, generally less than 5 m deep, with the exception of the ship channel which reaches a maximum of 15 m depth. The estuary includes Nueces Bay, Oso Bay, Corpus Christi Bay, the northern portion of the upper Laguna Madre, and the southern portion of Redfish Bay (Figure 1). The main fluvial flow into this estuary is from the Nueces River. The estuary is separated from the Gulf of Mexico by the barrier beach island, Mustang Island, with one main tidal pass, Aransas Inlet. A secondary and possibly more influential access to Gulf waters is through the extensive Laguna Madre to the south of the Corpus Christi Bay estuary (Smith 1978).

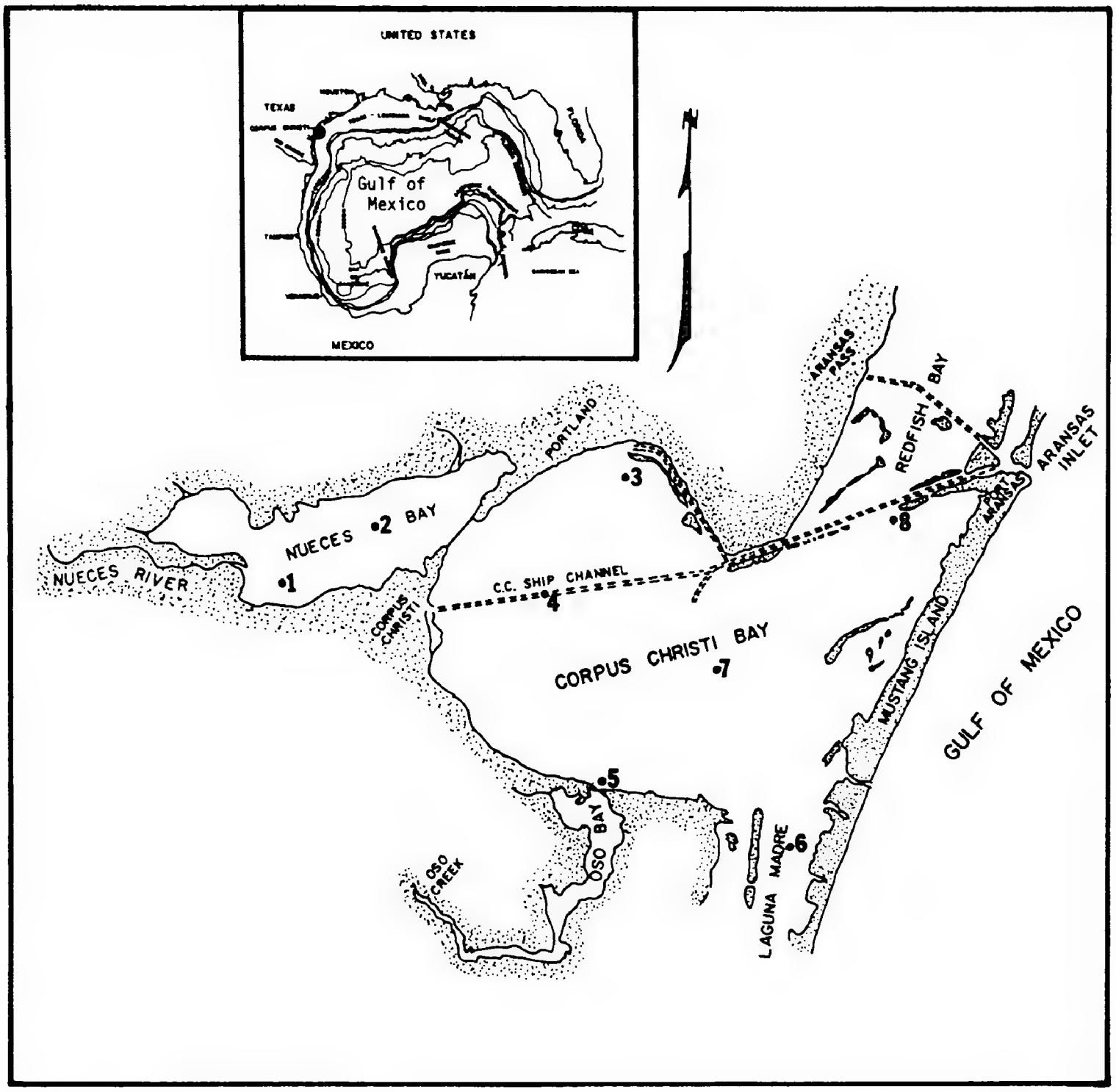

FIG. 1. Map of Corpus Christi Bay estuary showing inclusive bodies of water. Sampling sites are also shown.

Both meteorological events and tides influence the Corpus Christi Bay estuarine circulation. The tidal range varies from a few centimeters at times of equatorial tides to as much as 30 cm during tropic tides (Smith 1977). Because the mean tidal change can be quite small relative to the volume of the estuary, many tidal cycles must occur before a significant fraction of the system is flushed by tidal processes (Smith 1982). Observations have indicated that changing wind conditions rapidly affect the estuary's circulation and associated turbidity patterns because of the shallow water depths (Shideler 1980). Because of the presence of winds on almost a daily basis, the estuary is almost always turbid. This estuary is also located in a semiarid region of the Texas coast and often receives less than 70 cm of rainfall annually (Flint and Rabalais 1981). Evaporation is usually high, often exceeding rainfall, which sometimes results in hypersaline conditions. Contrasted to the size of the estuary, the riverine input from the Nueces River is small and seasonal in nature (Flint, *et al.* 1982). Therefore, this estuarine ecosystem is relatively sensitive to changes from such factors as surges of freshwater input and

often responds rapidly to such events. An example of a more catastrophic change would be from an event such as a tropical storm or hurricane.

A three-year study of phytoplankton species assemblages in the Corpus Christi Bay estuary (Holland, Maciolek, Kalke, Mullins, and Oppenheimer 1975) indicated that the dominant flora were diatoms. *Thalassionema nitzschioides, Thalassiothrix frauenfeldii,* and *Chaetoceros* sp. were the dominant species, while diatoms in general comprised more than 70% of the total phytoplankton community over the three-year study. Exceptions to diatom dominance were occurrences of the blue-green algae, *Anabaena* sp. and *Oscillatoria* sp. during the fall, especially in Nueces Bay. Maximum phytoplankton mean abundances were observed in the winter and early spring at approximately 1000 cells/ml. Minimum abundances usually occurred in the summer and early fall at less than 100 cells/ml.

Other potential sources of the photosynthetic production of new organic matter to this estuary come from surrounding *Spartina* marshes, submerged seagrass beds and algal mudflats of the estuary. Approximately 182.1 km^2 of marshes surround the Corpus Christi Bay estuary and contribute 9.5×10^6 kg C/yr (Armstrong 1982). Seagrass beds cover 51.6 km^2 of the estuary bottom, and between seagrass blades and associated epiphyte production, provide approximately 53.9×10^6 kg C/yr (Morgan and Kitting in press). Algal mudflats, which comprise approximately 22.7 km^2 of the Corpus Christi Bay estuarine ecosystem, contribute an additional estimated 6.0×10^6 kg C/yr (W. Pulich, personal communication).

METHODS

Eight sampling stations were established in the Corpus Christi Bay estuary (Figure 1). The stations were located such that a spatial change from river-influenced estuary to ocean-influenced estuary was sampled during each data collection period. Two stations were located in Nueces Bay (Stations 1 and 2), Station 5 characterized the dynamics of Oso Bay at its input to Corpus Christi Bay, Station 6 characterized the upper Laguna Madre, and the remaining four stations represented Corpus Christi Bay open-water locations. These stations were sampled in June and July 1981, and then every three months (quarterly) from October 1981 to October 1983.

Upon arrival at a station, Secchi depth, temperature, salinity, pH (Hydrolab Surveyor 6) and nutrient samples were obtained to characterize the water column. Secchi depth was used to determine the depth of the photic zone (1% light level) according to methods of Parsons, Takahashi, and Hargrave (1977, p. 102). From salinity, temperature and pH data, the total carbon dioxide of the water column at each station was estimated (Harvey 1966) for use in primary productivity estimates (Goldman 1968). On numerous occasions these CO_2 calculations were contrasted to alkalinity measures at the stations and similar results were observed. Water column temperature or salinity stratification was never observed during this study at any station.

Ammonia-nitrogen was measured here because (1) it is one of the preferred forms of nitrogen by phytoplankton (Eppley, Packard, and MacIsaac 1970; McCarthy and Eppley 1972) and (2) nitrate-nitrogen concentrations were usually undetectable when measured. At each station triplicate water samples were obtained at 1 m water depth and placed in 60 ml acid-washed bottles for laboratory ammonia-nitrogen determination. Water samples for ammonia-nitrogen analysis were also obtained 3 km upstream from the mouth of the Nueces River. All samples were immediately fixed in the field with phenol (0.4 g/100 ml sample) as a preservative (Degobbis 1973). In the laboratory all ammonia-nitrogen samples were immediately analyzed by the phenolhypochlorite method of Solórzano (1969).

At each station water samples were obtained for phytoplankton production measurements (mg $C/m^3/h$) at 0.5 m and 1.0 m depth and placed in 4 l opaque bottles. Usually within 1 hr of collection water was transferred from the opaque storage bottles (after shaking) to 125 ml hard-glass reagent bottles with teflon caps for incubation. Each station/depth was represented by one opaque and two light incubation bottles. Prior to *in situ* incubation at the original sampling depths, each bottle was inoculated with 4 μCi/ml of $NaH^{14}CO_3$ and mixed thoroughly. Incubations were conducted at two index sites on successive days. Station 2 (Figure 1) was the index

site representing Nueces Bay collection sites and Station 7 was the index site representing Corpus Christi Bay sites. The index sites were judged to be similar in water quality (*e.g.*, turbidity) to all other sites from which samples were obtained and incubated at the index sites. *In situ* incubations occurred from 1000–1400 hr. Incubations were ended by filtration through 0.45 μm Millipore filters.

After filtration, the filters were rinsed with slightly acidified distilled water to remove dissolved forms of the isotope and placed wet directly into scintillation vials containing 15 ml ScintiVerse cocktail for counting on a Packard tri-Carb Liquid Scintillation Spectrometer (#3255). Counting efficiency was estimated from the channel ratio, a calibrated quenched series, and ^{14}C-labelled toluene of known radioactivity. Efficiency usually ranged from 70–82%. Daily light intensity during production incubations was measured by a Weathertronics Pyranograph (#3010) and expressed in Langleys/day (g-cal/cm^2/day). Daily primary productivity (mg C/m^2/day) was calculated from the ratio of incubation period light intensity to daily light intensity, and from depth of the photic zone, which was derived from Secchi depth measurements or station depth, whichever was less.

Other environmental data used for comparison during these studies included wind speeds, precipitation, and evaporation rates from the NOAA Local Climatological Data Summary for Corpus Christi, Texas. Riverine flow rates from the Nueces River were obtained monthly from the Texas Department of Water Resources (M. Lynn, personal communication).

RESULTS

ENVIRONMENTAL CHARACTERIZATION

The range in most physical environmental variables measured for the study area between sampling periods was quite broad (Figure 2). Salinity showed the greatest amount of annual variation of those hydrographic variables measured. The 1981 mean salinity for the entire Corpus Christi Bay estuary was 20.1 ppt. In contrast, 1982 mean salinity rose to 28.4 ppt and although the 1983 salinity mean (28.8 ppt) was also high, salinities later in this study year decreased significantly ($P < 0.05$) from 1982 and earlier 1983 salinity ranges. Water temperatures ranged from around 12°C in the winter to peaks near 30°C in the summer (Figure 2) and were similar in all three study years. Daily solar radiation on the estuary's surface peaked in July each year and exhibited minimum values in January and February.

Local rainfall in the Corpus Christi Bay estuary varied significantly over the three years of study (Figure 2). The total rainfall for 1981 was 111.8 cm. In 1982 the rainfall total was half of 1981 with 57.1 cm measured. In 1983 the precipitation total increased again to 95.0 cm with much of this rain occurring in the summer and fall of 1983 (Figure 2). Nueces River gauged flow corresponded to rainfall patterns early in the study period but did not show the same peaks as precipitation during later study intervals, especially in 1983 (Figure 2). The overall pattern of lower precipitation and less riverine flow in 1982 also corresponded to much higher salinities during this year in the Corpus Christi Bay estuary.

STATION PRIMARY PRODUCTIVITY VARIATION

The sampling sites used to characterize phytoplankton productivity of the Corpus Christi Bay estuary varied a great deal in water depth (Figure 3). In

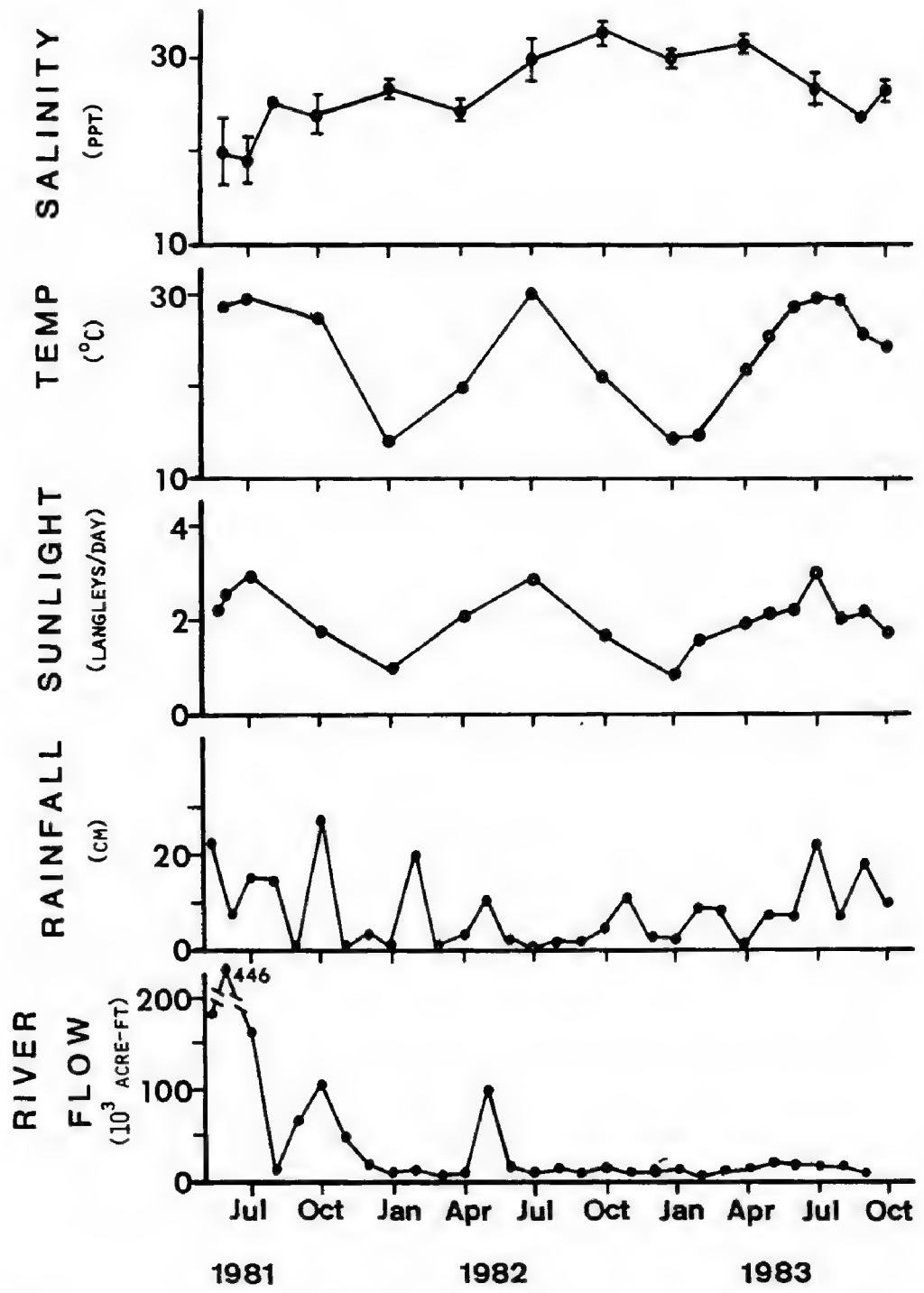

FIG. 2. Plots of hydrologic and meteorologic variables measured during the Corpus Christi Bay estuarine study. Salinity and water temperature represent the averages of all eight stations.

all cases this variation in depth correlated with variation in Secchi depth ($r = 0.56$) at the respective stations (Figure 3). As water depth increased Secchi depth was usually greater, indicating a deeper photic depth for primary productivity to occur. This was usually the case for the deeper more centrally-located stations (Stations 3, 4, 6, and 7). Differences in salinity between stations were usually noted. The Nueces Bay sampling sites (Stations 1 and 2) usually exhibited lower salinities than the Corpus Christi Bay sites during most sampling periods (Figure 3). With the exception of Station 5, which was located at the mouth of Oso Bay and near a sewage outfall site, ammonia-nitrogen concentrations of the water column did not differ between most stations. Station 5 exhibited a mean for ammonia,

however, that was three times greater than any other station mean during the entire study (Figure 3).

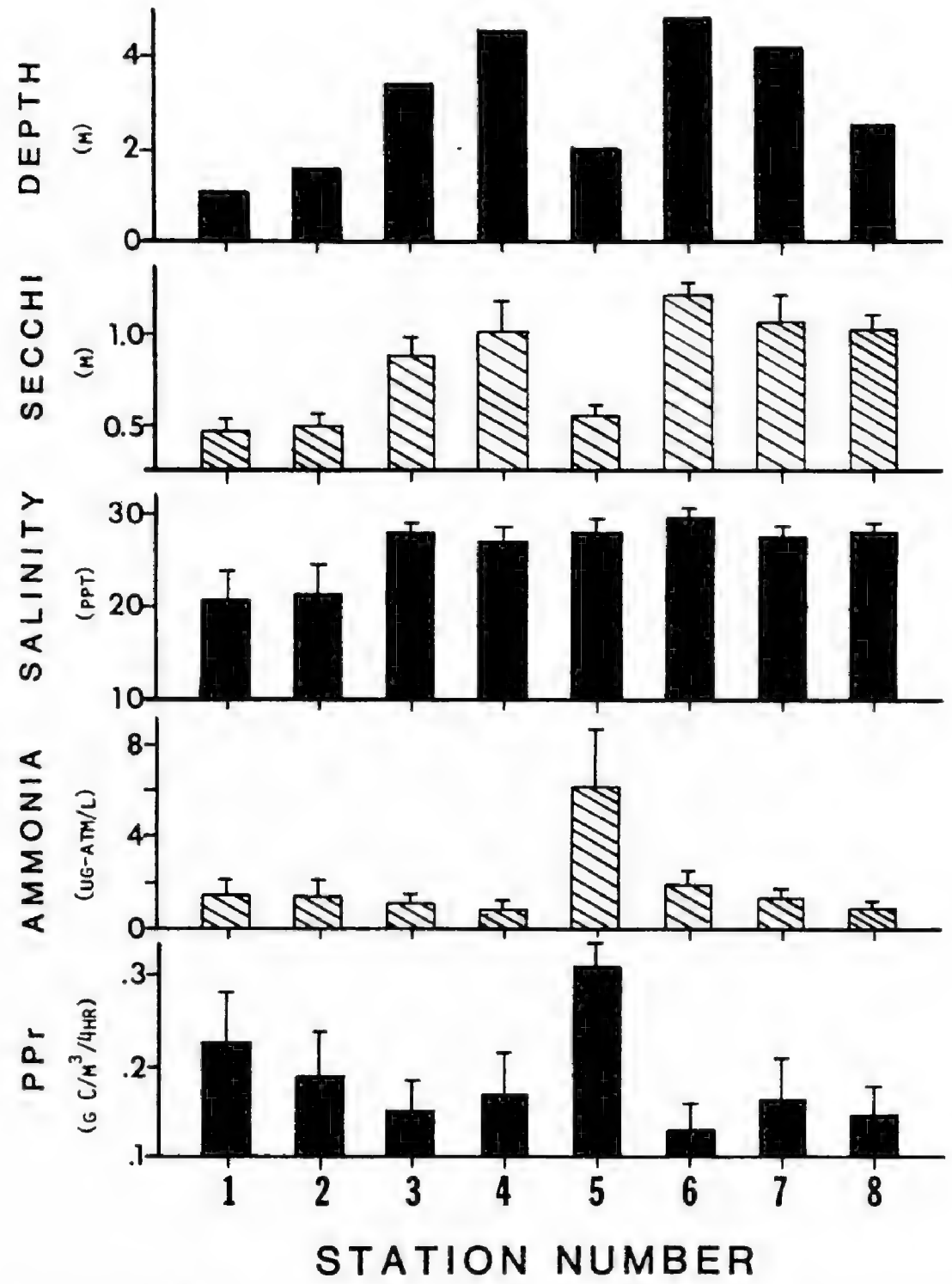

FIG. 3. Study means for various water quality variables and primary production measured at each sampling site in the Corpus Christi Bay estuary. Standard errors of the means are indicated by the lines above the bars.

Differences for 4-hr incubation rates of phytoplankton productivity between the 8 sampling sites were judged to be significant ($P < 0.05$) over the total study period according to ANOVA. Major difference in rates occurred for the Nueces Bay sampling sites (Stations 1 and 2) and Station 5, which exhibited the largest mean rate of all stations observed (Figure 3). Nueces Bay sites almost always showed greater 4-hr rates than middle-bay Corpus

Christi sites. Variability over the total study period in primary productivity was also much greater at the upper-estuary (Nueces Bay) sites than within the main part of the estuary. For example, coefficients of variation for Station 1 and Station 2 mean primary production rates were 100% and 93% respectively. In contrast, all the other study site coefficients of variation ranged between 65% and 79%.

The calculation of study period mean daily primary productivity rates for the eight sampling sites showed a different trend with respect to estuary production than did the 4-hr incubation rates (Figure 4). When the

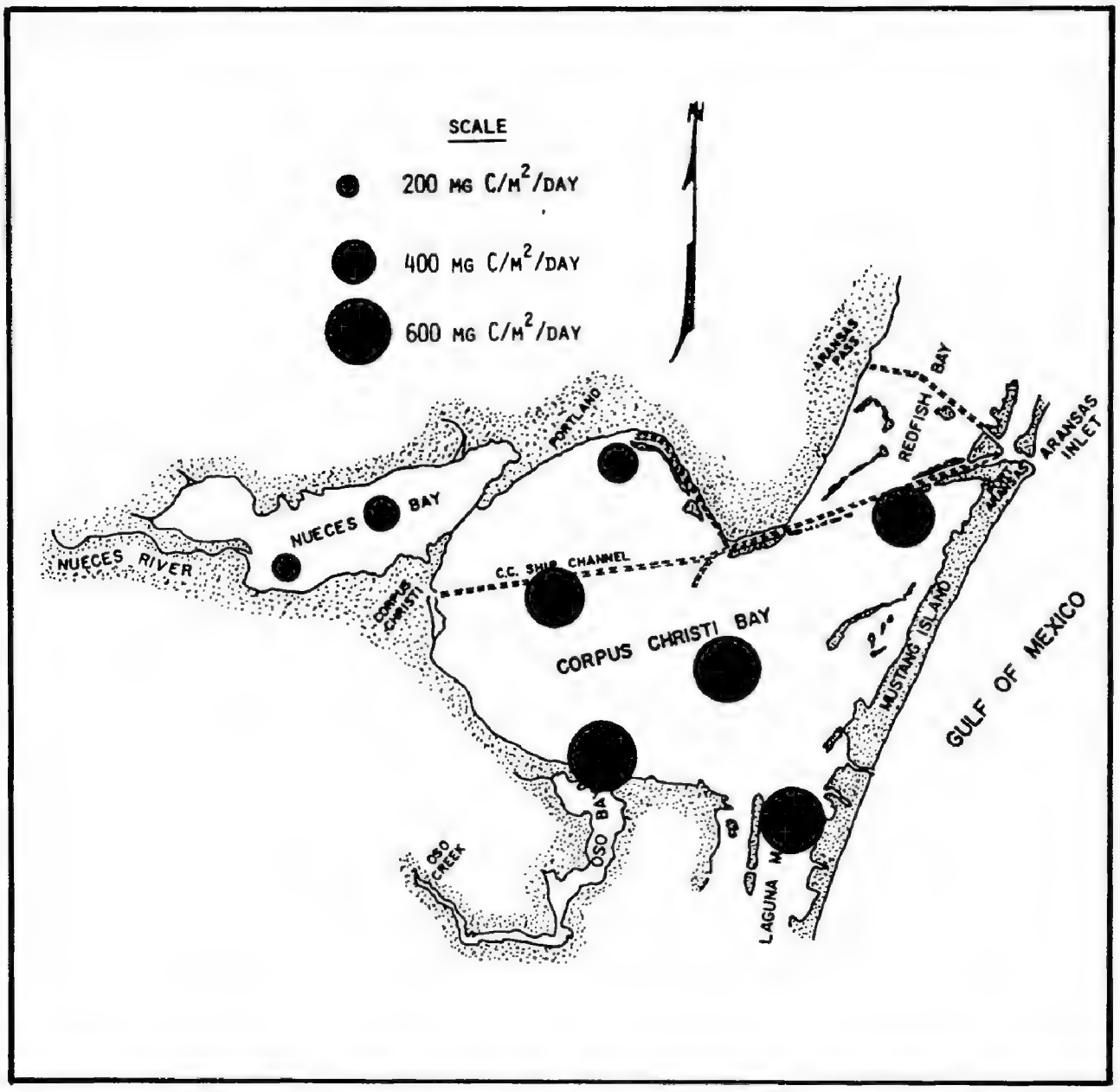

FIG. 4. Spatial variation in mean daily primary productivity estimated for the entire study period in the Corpus Christi Bay estuary.

shallower water depths and shallower Secchi depths of Nueces Bay were considered (Figure 3) in the daily production measures, total water column phytoplankton production was less in Nueces Bay than at any other station (Figure 4). In general, the estimates of mean daily production over the entire study period illustrated that sites in the estuary farther away from the river

were more productive than sites closer to the river. The one exception was Station 5 which showed the greatest mean daily rate, corresponding to highest ammonia-nitrogen concentrations in the estuary.

Regression analyses were conducted on the phytoplankton primary productivity data at each sampling site, using independent environmental variables that best characterized (differentiated) each site, in order to identify variables that potentially influenced the observed spatial patterns for production throughout the estuary. Because seasonal variation in primary productivity due to temperature and solar radiation might obscure other environmental factors influencing spatial productivity patterns, the regression analyses were performed separately on similar sampling months. The results indicated that January and July productivity measurements were most correlated to water column ammonia-nitrogen concentrations (Figure 5). April and October phytoplankton productivity variation on the

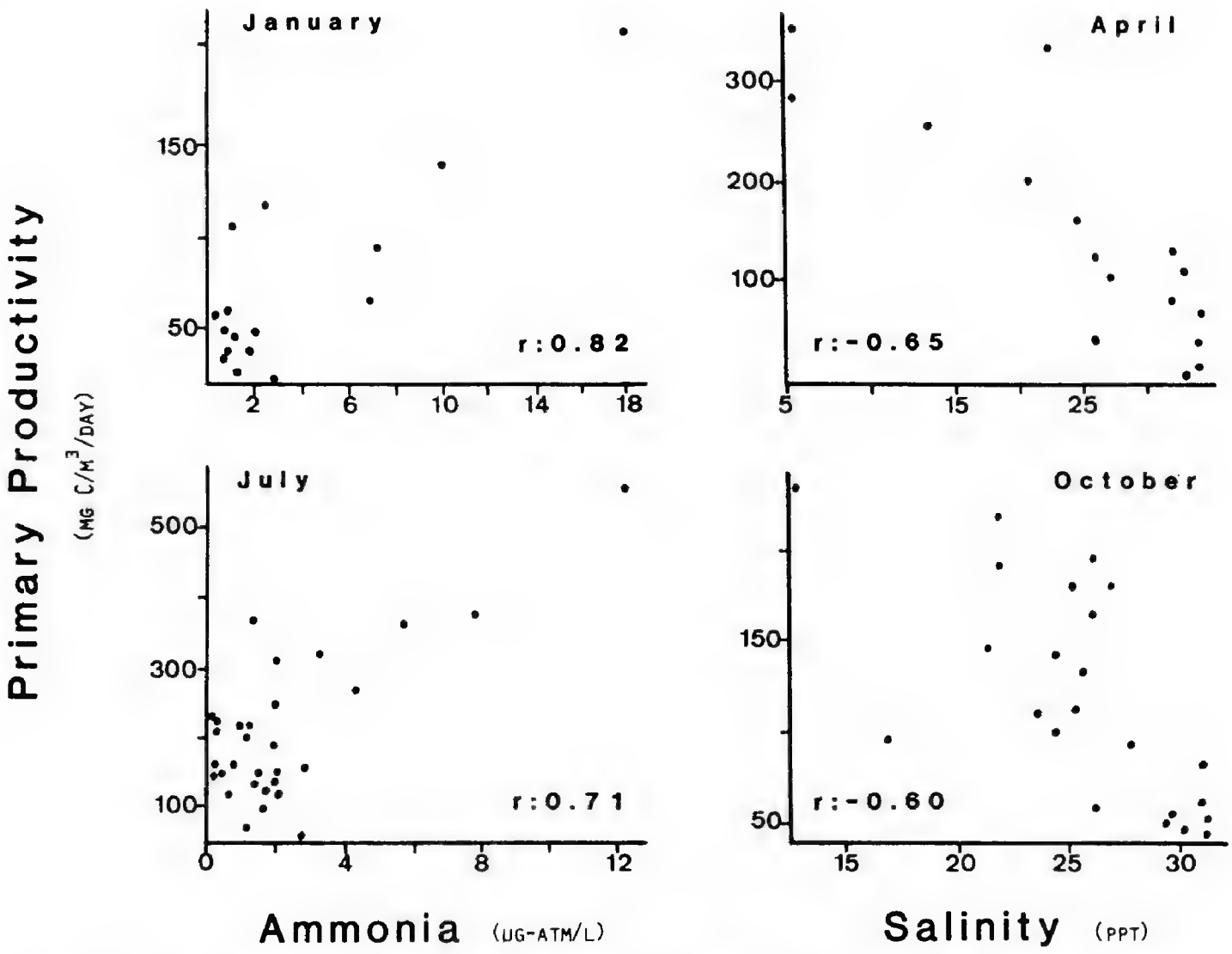

FIG. 5. Scatter plots of environmental variables determined as most influential to primary productivity variation by regression analysis for the four seasons of the year. Correlation coefficients for each plot are indicated.

other hand was most correlated with differences in salinity, which indicated that some sites were more influenced by freshwater input than others. In contrast, correlations for productivity with salinity in January and July and

productivity with ammonia-nitrogen concentrations in April and October never exceeded $r = 0.32$.

Although changes in phytoplankton production at increasing depths in the water column would be strongly influenced by turbidity, it was thought that nutrient availability might also be influential. Therefore, turbidity, as measured by Secchi depth, and water column ammonia-nitrogen variations were both compared to the ratio of production between 0.5 m and 1.0 m depths at each station using regression analysis to determine which independent variable showed stronger correlations. These analyses indicated that Secchi depth and water column ammonia-nitrogen were both significant ($P < 0.05$) in explaining observed variation in this ratio. Approximately 56% of total variation (multiple R^2) in the change of production with increasing depth was explained by Secchi depth and ammonia, with Secchi depth alone accounting for 43% of this variation ($r = 0.66$).

ANNUAL PRODUCTIVITY PATTERNS

A significant difference ($P < 0.001$) was observed between the two major components of the Corpus Christi Bay estuary, Nueces Bay and Corpus Christi Bay, for daily phytoplankton primary productivity rates compared annually using two-way ANOVA, where one factor was station location (Nueces Bay or Corpus Christ Bay) and the other factor was sampling year (1981, 1982, or 1983). Figure 6 illustrates the difference in productivity between Nueces Bay and Corpus Christi Bay for each sampling period and also shows how productivity varied over the entire study interval. Primary productivity was much greater during 1981 than for either 1982 or 1983 study years. The mean annual production rate of the entire estuary for 1981 was 717.2 mg C/m²/day. It should be noted, however, that the mean annual rate did not include the winter period for 1981 which might have decreased the annual mean considerably. For example, if 1982 and 1983 winter measures were used to calculate a mean winter rate to be included in the 1981 annual estimate, then the 1981 productivity measure would be decreased to 546.2 g C/m²/day. In contrast to the 1981 measures, mean productivity rates of the entire estuary for 1982 and 1983 were 346.8 and 421.8 mg C/m²/day respectively. Another pattern to note from Figure 6 was that the summer and fall rates for 1983 were greater than for 1982, which was the major reason why the 1983 overall estuarine mean was greater.

A consistent seasonal pattern was not evident in the daily phytoplankton productivity rates for the Corpus Christi Bay estuary (Figure 6). The winter sampling periods usually showed the lowest rates in Corpus Christi Bay, but this was not true for Nueces Bay in 1983 when the spring period exhibited the lowest rates observed during the entire study for both bays. This low production measure corresponded to Secchi depths of 0.2 m in Nueces Bay, which were also the shallowest measurements for this variable during the entire study. For all stations together over all three measurement years, the grand mean phytoplankton productivity rate for the Corpus Christi Bay estuary was 479.9 mg C/m²/day or 174.1 g C/m²/yr.

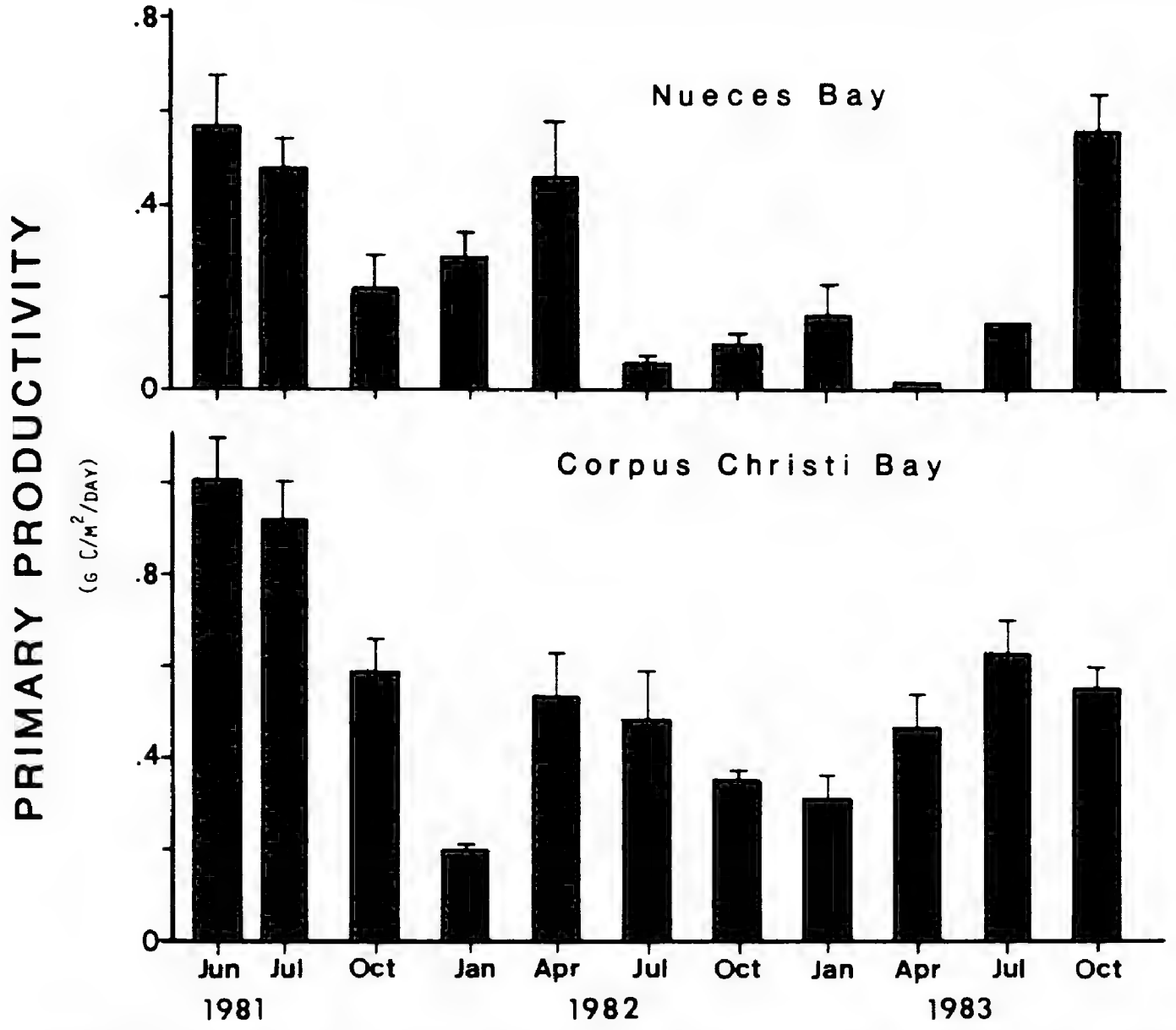

FIG. 6. Mean daily primary productivity rates of Nueces Bay and Corpus Christi Bay sampling sites for each collection interval of the three-year study period. Lines above bars represent standard errors of the means.

Multiple regression analyses were again employed to detect general environmental variables that may serve as influential factors in regulating overall primary productivity in this estuary. Because productivity was significantly different between Nueces and Corpus Christi Bays, it was thought that different environmental variables may be causing the variation observed. Therefore, regression analysis was conducted separately on productivity measures from each bay area.

Table 1 illustrates the results of these analyses. Nueces River flow was the most strongly correlated environmental variable with primary productivity rates for Nueces Bay. This variable alone explained 47% of the variation in productivity. Secchi depth, indicative of water turbidity, explained another 19% of the variation in Nueces Bay productivity. Riverine total inorganic nitrogen input and mean monthly wind speeds, which may influence Secchi depth but was not observed to be strongly correlated here, explained an additional 12% of the total observed variation in Nueces Bay productivity.

TABLE 1

Regression analysis of Nueces Bay and Corpus Christi Bay daily primary productivity measures with a total of nine environmental variables measured simultaneously. Only significant independent environmental variables are shown.

Dependent Variable - Surface daily primary productivity (mg C/m³/day)			
Independent variables	R^2	r	Significance
	NUECES BAY		
River flow	0.468	0.684	0.02
Secchi depth	0.666	0.425	0.01
River nitrogen	0.725	0.377	0.02
Winds	0.787	-0.160	0.03
	CORPUS CHRISTI BAY		
Rainfall	0.784	0.885	0.00
Average sunlight	0.899	0.759	0.00
Secchi depth	0.950	-0.461	0.00
Water column ammonia	0.960	0.208	0.01

R^2 - Multiple regression coefficient of determination

r - Simple correlation

Monthly rainfall was the most strongly correlated environmental variable with Corpus Christi Bay primary productivity rates (Table 1) and explained 78% of the total observed variation in this dependent variable. Daily sunlight and water turbidity explained another 17% of the variation in productivity. Ammonia-nitrogen in the water column also was significant in the regression analysis of Corpus Christi Bay primary productivity; it explained an additional 1% of observed variation.

DISCUSSION

The data on primary productivity of the Corpus Christi Bay estuary collected during this three-year study illustrated the pattern of biological response to short-term physical forcing events that one would expect in an ecosystem sensitive to acute change. As described previously, this estuarine ecosystem has low riverine input and small tidal exchanges, both of which contribute to very long turnover times for the estuary (Smith 1982). As a result, productivity of the estuary appeared to be dominated by meteorologic and hydrologic events as illustrated in Table 1. Changes in phytoplankton nearest the Nueces River were most correlated with freshwater flow from this river. Likewise, changes in phytoplankton more centrally-located in the estuary were most related to rainfall inputs of freshwater and associated nutrients, either through the precipitation directly or indirectly through land runoff. Related to these patterns of riverine and rainfall influences were the

sources of nitrogen most affecting productivity. In Nueces Bay riverine nitrogen contributed to the observed variation in primary productivity rates (Table 1). In Corpus Christi Bay, farther from the river mouth, nitrogen measured in the water column was significantly correlated with primary productivity rates. Water column nitrogen concentrations were in turn at least partially affected by localized land runoff.

Further evidence of this meteorologic and hydrologic forcing of primary productivity comes from visual comparison of monthly rainfall and river flow rates (Figure 2) with primary productivity rates of both Nueces and Corpus Christi Bays (Figure 6). Nueces Bay productivity appeared to be most sensitive to peaks in freshwater flow from the river. Corpus Christi Bay productivity, on the other hand, paralleled rainfall increases, which was especially apparent during the latter half of 1983. The results of this study suggested that during periods when no major increases in freshwater input were observed (*e.g.*, late 1982 and early 1983), the estuary exhibited lowest productivity rates. When high precipitation or fluvial flow did occur, however, the biologic response in terms of increased productivity was immediate (Figures 2 and 6) and probably maintained itself in a steady state in the system over the long term in respect to food resources for other trophic levels.

Acting synergistically with the dominating influences of river flow and rainfall on primary productivity were seasonal variability and water turbidity. Solar radiation was shown to strongly affect the seasonal patterns of productivity observed (Table 1). This factor was most responsible for the annual peaks in production that occured in the late spring and summer (Figure 6, Corpus Christi Bay). Although primary production rates measured over the incubation period (mg C/m^3/4 hr) were usually greater in Nueces Bay than Corpus Christi Bay (Figure 3), with the exception of Station 5, the overall pattern exhibited was greater productivity (mg C/m^2/day) at the lower stations (more oceanic) in Corpus Christi Bay (Figure 4). This trend occurred because these sites were less turbid and deeper, and provided a greater photic zone, in which phytoplankton photosynthesis could occur.

The indication that water column turbidity limits the amount of primary production realized by the Corpus Christi Bay estuary, both from the regression analyses (Table 1) and the comparison of 0.5 m with 1.0 m production rates, best illustrated why this estuarine ecosystem is not as productive as others around the world. Based upon data from a number of estuaries around North America (Table 2), the Corpus Christi Bay estuary was relatively oligotrophic in comparison. The greatest annual primary productivity for an estuary was estimted at 532 g C/m^2/yr in British Columbia (Stockner and Cliff 1979). In contrast, the least productive estuary was a New England coastal embayment that exhibited 50 g C/m^2/yr (Marshall 1970). The Corpus Christi Bay estuary, which over a three-year study period (86 station/time measurements) exhibited a mean phytoplankton productivity rate of 174.1 g C/m^2/yr, was at the lower end of the scale illustrated in Table 2.

TABLE 2

Annual phytoplankton primary production estimates for selected estuarine ecosystems in North America.

Estuary	Primary Production (g C/m²/yr)	Reference
Port Moody Arm, British Columbia	532	Stockner and Cliff 1979
Pamlico River, North Carolina	500	Kuenzler *et al.* 1979
Puget Sound, Washington	465	Winter *et al.* 1975
Great South Bay, New York	450	Lively *et al.* 1983
New York Bight, Mid-Atlantic	370	Malone 1976
Straight of Georgia, British Columbia	345	Stockner *et al.* 1979
Three North Carolina Estuaries (average)	320	Fisher *et al.* 1982
Beaufort Channel, North Carolina	225	Williams and Murdock 1966
Narragansett Bay, Rhode Island	220	Smayda 1957
Upper New York Harbor	200	Malone 1977
Peconic Bay, New York	162 - 213	Bruno *et al* 1980
St. Margaret's Bay, Nova Scotia	190	Platt 1971
Corpus Christi Bay, Texas	174	Present Study
Georgia Bight	171	Haines and Dunston 1975
Newport River Estuary, Virginia	110	Peterson and Peterson 1979
Wassaw Sound, Georgia	90	Turner *et al.* 1979
New England coastal estuary	50	Marshall 1970

Several other estimates of phytoplankton productivity in Texas estuaries have been calculated from various studies over the past 20 years. Most of these studies, however, used the oxygen method (Strickland and Parsons 1972) for measuring photosynthesis of estuarine phytoplankton. It is thought that the oxygen method more closely measures gross production of plankton while the ^{14}C method, employed here, more accurately measures net plankton production (Strickland and Parsons 1972). Therefore, in order to make comparisons between the present study and previous studies on Texas estuaries, it was assumed that the ^{14}C method measured only 70% of that carbon production (1 g carbon fixed equals 3 g oxygen released; Finenki and Zaika 1970) measured by the oxygen method (Riley and Chester 1971). Thus, all previous oxygen estimates of primary productivity in Texas estuaries were decreased by 30%.

The comparison of these measures with productivity estimates from the present study are illustrated in Table 3. The present study estimated phytoplankton daily productivity to be well below measures between 1960–62 for the Corpus Christi Bay estuary. In addition, Corpus Christi Bay was shown to be the least productive of all Texas estuaries when the present study data were compared to study results on other Texas estuaries (Table 3). It was interesting to note, however, that if the estimates for Galveston Bay, Corpus Christi Bay between 1960–62, and the Laguna Madre from Table

TABLE 3

Comparison of phytoplankton primary production rates for various Texas estuaries.

Estuary	Primary Production[1] (g C/m²/day)
Galveston Bay [2]	4.11
San Antonio Bay[3]	0.70
Corpus Christi Bay [4] (1960 - 62)	1.76
Corpus Christi Bay (present study)	0.48
Upper Laguna Madre [4]	2.68
Lower Laguna Madre [4]	4.78

[1] Where photosynthesis was initially measured by oxygen production, oxygen production was converted to carbon fixation based upon ratio of 3:1 (Findko and Zaika 1970). Oxygen production measures gross production; to convert to net production which is more closely estimated by Carbon-14 method, assumed net production was 70% of gross production (Riley and Chester 1971).

[2] Armstrong and Hinson (1973).

[3] Davis (1971).

[4] Odum and Wilson (1962); Odum *et al.* (1963).

3 were expanded to a yearly rate, annual estimates of phytoplankton productivity would then range from 642 g C/m²/yr in Corpus Christi Bay to 1,744 g C/m²/yr for the lower Laguna Madre. Comparison of these annual estimates with other estuaries in Table 2 indicated that Texas estuaries would then be up to three times more productive than any other estuaries reported. Considering the highly turbid conditions of most Texas estuaries, however, these measures were probably not accurate and/or representative of annual production. The estimates for primary productivity of the Corpus Christi Bay estuary from the present study more precisely placed Texas estuaries in the proper perspective in comparison with other estuaries around North America.

There are a number of carbon sources available to the Corpus Christi Bay estuary besides the primary production of organic matter by phytoplankton photosynthesis. For example, two other potential contributors are seagrass beds and their associated epiphyte algae and *Spartina* salt marshes, both of which comprise a major surface area of the total estuary (see STUDY AREA). Armstrong (1982) estimated that *Spartina* salt marshes contributed approximately 52.2 g C/m²/yr to the open-water habitat of the Corpus Christi Bay estuary. Furthermore, it was calculated that seagrass/epiphyte primary productivity contributed 94.2 g C/m²/yr to the total estuarine habitat (Morgan and Kitting in press). In addition, studies on tidal flats near the Corpus Christi Bay estuarine area (W. Pulich, personal communication) estimated that approximately 13.9 g C/m²/yr was transported from this biotope to the open-water habitat. All these carbon sources combined with phytoplankton productivity represented an annual primary production estimate of 334.4 g

$C/m^2/yr$ for the Corpus Christi Bay estuary. Phytoplankton productivity contributed 52% of the total estimated production for this estuary, based upon these calculations.

In contrast, Lively, Kaufman, and Carpenter (1983) estimated the phytoplankton contribution of carbon for the Great South Bay (New York) to be 85% of all sources. Marshall (1970) calculated phytoplankton carbon contributions to be 11% of all other carbon sources in a New England coastal estuary. Bahr, *et al.* (1982) estimated that phytoplankton productivity respresented 47% of total carbon productivity in Louisiana estuaries.

From the regression analysis results it was suggested that variation in nutrients from at least two sources (rainfall/runoff and river flow) contributed to the patterns observed for primary production in the Corpus Christi Bay estuary. Inwelling of nitrogen from coastal continental shelf waters contributed very little "new" nitrogen to this estuary because of the small tidal amplitudes common in this region of the Gulf of Mexico (Smith 1982). The major source of "new" nitrogen to the Corpus Christi Bay estuary was through input from the Nueces River. Measurements between 1972–75 (Texas Department of Water Resources 1981) and measurements from the present study indicated that the average total inorganic nitrogen input from the Nueces River was 3.79×10^5 kg/yr. The measured primary productivity rate for phytoplankton in the estuary was 174.1 g $C/m^2/yr$ or 26.4 g $N/m^2/yr$ if we assume a C:N ratio of 6.6 for phytoplankton (Redfield, Ketchum, and Richards 1963). Therefore, riverine input of nitrogen could provide only 3.3% of the nitrogen needed by open-water phytoplankton productivity in this estuary.

In contrast, from measures of benthic nutrient regeneration in this estuary (Flint, *et al.* 1982; Flint, Kalke, and McCoid 1983) it was estimated that annually the sediments were able to supply 23.9 g $NH_4^+ - N/m^2$. Thus, the sediments through nutrient recycling could potentially provide approximately 90% of the nitrogen needed by phytoplankton for photosynthesis in this estuary. Oppenheimer, Isensee, Brogden, and Bowman (1975) indicated that point-source effluents as well as urban and agricultural runoff, provided approximately 9.3×10^5 kg/yr of nitrogen to the Corpus Christi Bay estuary. This accounted for 8% of the nitrogen needed for phytoplankton photosynthesis annually and with the other two nitrogen sources discussed above (riverine and sediment recycling) potentially could provide all nitrogen needed to support average phytoplankton productivity in the estuary.

The above discussion suggests that productivity of the Corpus Christi Bay estuary is sustained primarily through recycling of nutrients. Since no system is so efficient that losses never occur however, the continued maintenance and long-term steady state of this estuary's productivity must depend on the periodic input of "new" nitrogen which has been demonstrated by the results of this study to occur through meteorologic and hydrologic forcing. The increased rainfall and/or riverine input that periodically occurs in the Corpus Christi Bay area serves as an acute stimulus which significantly alters primary productivity, replaces lost materials to the

system, and allows recycling to again become the dominant forcing factor until the next acute change occurs.

ACKNOWLEDGMENTS

The author would like to thank R. Kalke and M. McCoid for field sampling assistance. Thanks are also extended to C. Goldman, T. Fisher and another anonymous reviewer for their constructive comments. Funding for this research was provided in part by the Texas Department of Water Resources and the Texas A&M University College Sea Grant Program through grants to The University of Texas at Austin Marine Science Institute at Port Aransas.

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SHORT NOTE ON CHANGES IN THE ABUNDANCE AND OCCURRENCE OF SIX MACROALGAL SPECIES ALONG THE TEXAS COAST OF THE GULF OF MEXICO

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ABSTRACT

Changes in the abundance and occurrence of six macroalgae collected from the jetties and the bay systems near Galveston, Port Aransas, and Port Isabel, Texas are noted. Both vegetative and reproductive plants of *Bryopsis pennata* are reported from the Galveston jetty for the first time.

Accepted 3 May 1984

INTRODUCTION

The occurrence and distribution of marine algae along the Texas coast of the Gulf of Mexico has been the subject of sporadic investigations over the last 50 years (see Edwards 1970, 1976, Edwards and Kapraun 1973, and Lowe and Cox 1978 for review of studies in the vicinity of Port Aransas and Baca, Sorensen and Cox 1979 for those near Port Isabel). Because of the varying, often lengthy, time intervals between these studies and because in some cases a study may represent the only extensive survey work at a particular site (*e.g.* Galveston by Lowe and Cox 1978), subtle changes in the flora or longer periodic cycles in algal distribution and occurrence may be overlooked. Although the marine algal flora on the Texas coast has in general remained fairly constant throughout this study period and compares well with earlier studies, comments on changing abundance and occurrence of six algae are reported here and will build on previous reports in order to contribute to the understanding of the algal flora of the Texas Gulf coast.

MATERIALS AND METHODS

Collections of seaweeds on the jetties and in the bays at Galveston, Port Aransas, and Port Isabel were begun seasonally in 1976 and continued to 1983. Many of these observations were

made by phycology students while participating in field trips under my direction, and their contribution to this report is gratefully acknowledged. The most intensive collections were made every other month from July 1977 to July 1980. Voucher specimens are deposited in the Department of Marine Biology Herbarium, Texas A&M University at Galveston, Galveston, Texas. Voucher specimens of *Bryopsis pennata* Lamour. are deposited in the herbarium of Dr. C. J. Dawes at the University of South Florida and at the Department of Biology Herbarium, Texas A&M University, College Station, Texas. Collection sites follow those used by other recent workers along the Texas Gulf coast (Fig. 1, for more detailed mapping of collection sites at

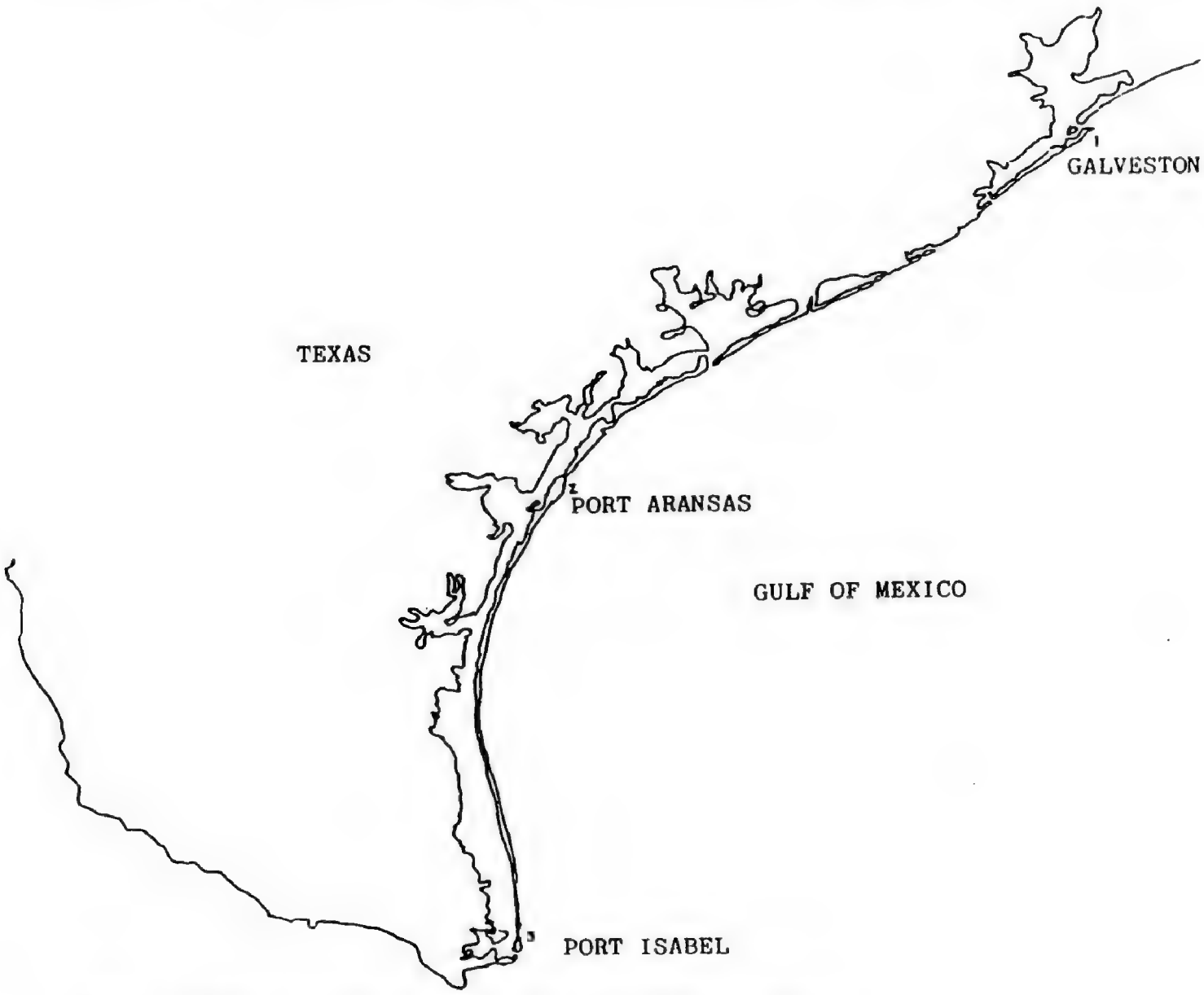


FIG. 1. Location of collecting sites along the Texas Gulf coast.

Galveston, see Lowe and Cox 1978; for Port Aransas, see Edwards 1970, 1976; and for Port Isabel, see Baca, Sorensen and Cox 1979).

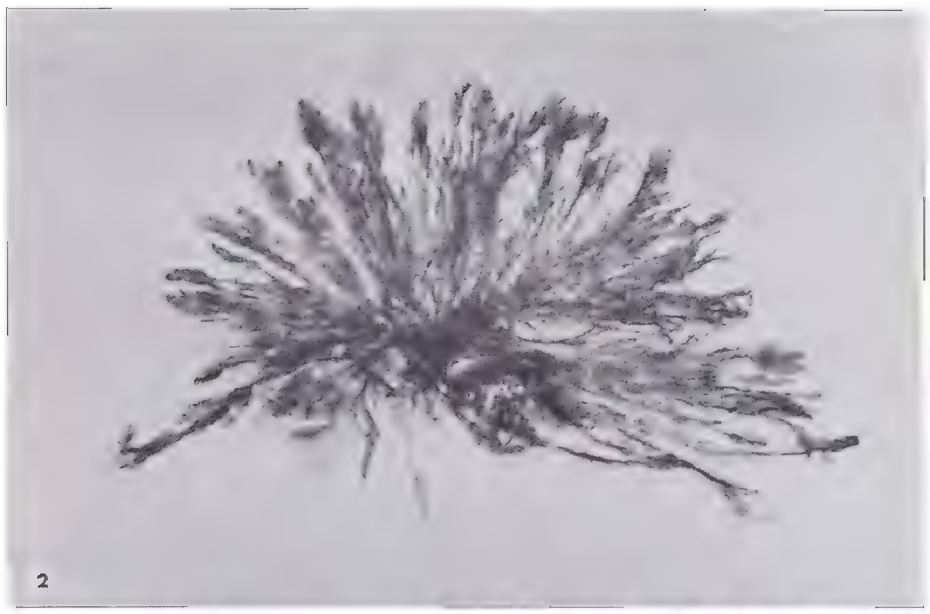
OBSERVATIONS AND DISCUSSION

GALVESTON JETTY

Bryopsis pennata Lamour. Small specimens of *B. pennata* were first collected on the jetty and on the fishing groins at 37th Street in January and February, 1982 and 1983 and on the jetty in February 1984. *B. pennata* had not been previously reported from the Galveston area (Lowe and Cox 1978).

Humm and Hildebrand (1962) reported *B. pennata* from Port Isabel, but Baca, Sorensen and Cox (1979) concluded that the small plants collected from bay or jetty habitats, which resembled *B. pennata,* were variations of *Bryopsis plumosa* (Hud.) C. Ag. Its appearance during the winter differs from the occurrence of *B. plumosa* and *Bryopsis hypnoides* Lamour., which are reported from Port Aransas and Port Isabel during the warmer parts of the year (Edwards and Kapraun 1973) and are not known from Galveston (Lowe and Cox 1978).

Both vegetative and reproductive plants were collected (Figs. 2–4) with



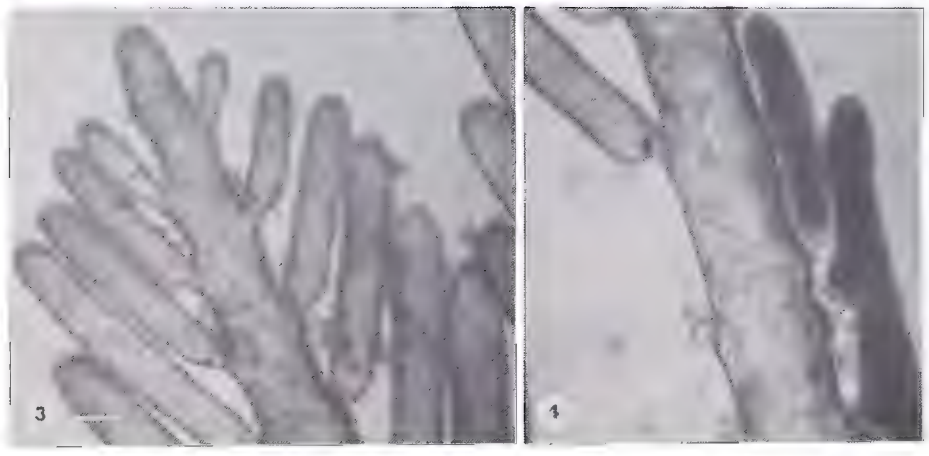


FIG. 2. *Bryopsis pennata*—herbarium specimen collected from Galveston, personal collection. Scale bar = 10 mm.

FIG. 3. *B. pennata*—vegetative branchlets. Scale bar = 90 μm.

FIG. 4. *B. pennata*—reproductive branchlets. Scale bar = 90 μm.

axes up to 20 mm and diameters *ca.* 225–445 μm. The branchlets are distichous in arrangement with an occasional radial pattern and arise from a matted base. The branchlets are restricted primarily to the ultimate portion of the upright branch. An average ratio of the length of the last branchlet to the first three branchlets on either side of the axis was 1:4.6; 1:2; 1:1.75 respectively, thus indicating that those branchlets near the tip of the branch are not noticeably shorter than those near the base of the branch. By comparison, a similar length ratio obtained for *B. plumosa* was 1:5.6; 1:4;

1:3.3, thus indicating the pyramid nature of the branchlets associated with this species. The branchlets of *B. pennata* are constricted at the base, a feature shared with *B. plumosa* but not with *B. hypnoides.*

A comparison of pyrenoid number within the plastid was made from living and dried material of *B. pennata* and from dried material of *B. plumosa* and *B. hypnoides* following Feldman (1937) (Figs. 5–12). In *B. pennata* the

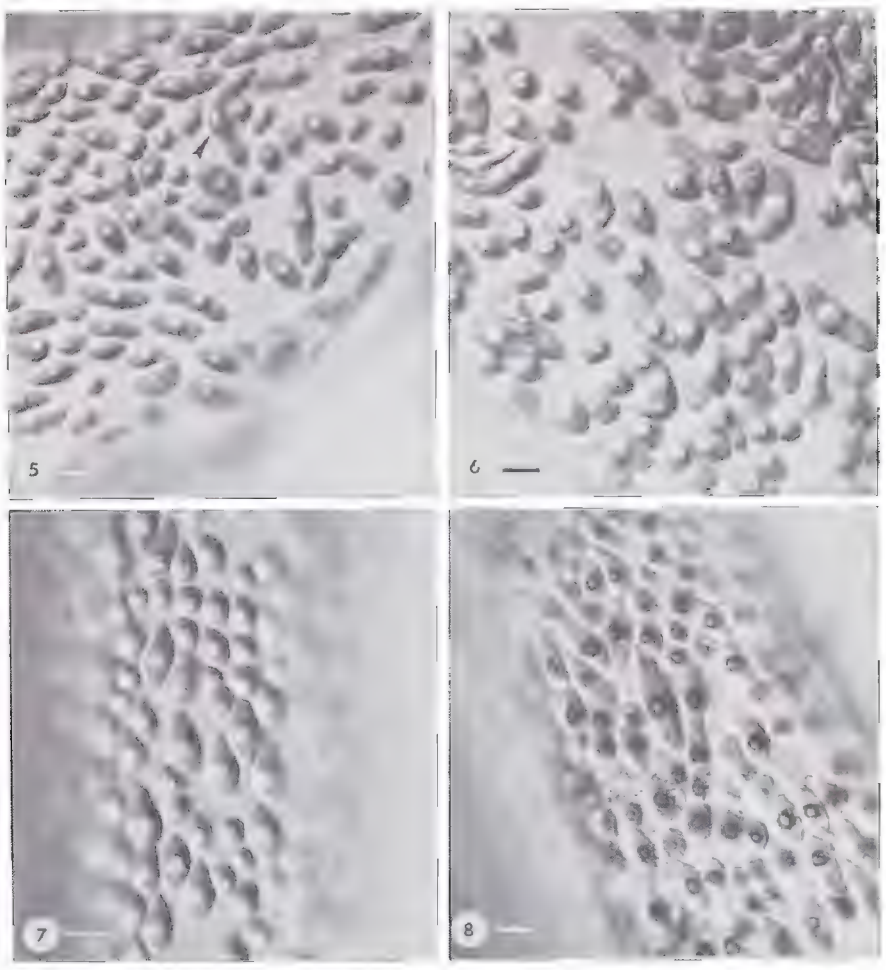


FIG. 5. *B. pennata*—plastids in older part of thallus. Arrow = 3 pyrenoids/plastid. Scale bar = 10 μm.

FIG. 6. *B. pennata*—irregular shape of plastids in intermediate part of thallus. Scale bar = 10 μm.

FIG. 7. *B. pennata*—rounder plastids near thallus tip. Scale bar = 10 μm.

FIG. 8. *B. pennata*—iodine staining of starch granules. Scale bar = 10 μm.

plastids were irregular in shape and contained 1–3 pyrenoids (Figs. 5–8). The most irregular shapes occurred in plastids found in the older parts of the thallus, while near the tips of the alga the plastids were more rounded (Fig. 7). The starch accumulated as compact plates around the pyrenoid. Observations on pyrenoid number from dried material stained with iodine were inconclusive, but occasionally a plastid containing multiple pyrenoids could be found (Fig. 9, arrow).

The plastids of *B. plumosa* were generally rounder and larger than those of *B. pennata.* They usually contained one pyrenoid, and the starch around the pyrenoid was more granular (Fig. 10). The plastids of *B. hypnoides* were smaller than the two previous species, and the single pyrenoid occupied a

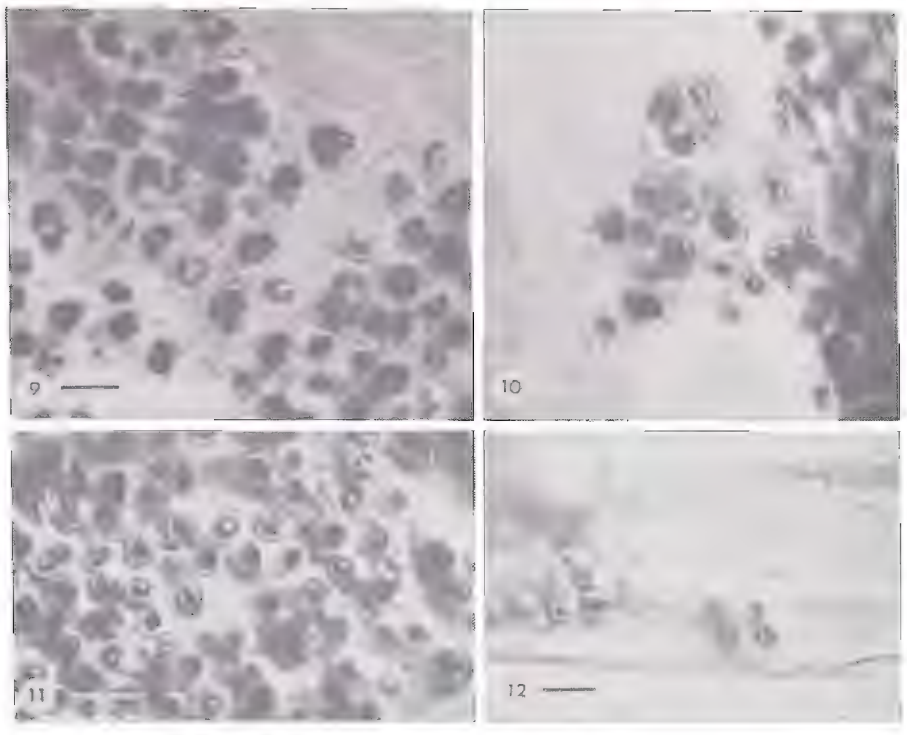


FIG. 9. *B. pennata*—dried material, rehydrated and iodine stained. Arrow = plastid with multiple pyrenoids. Scale bar = 10 μm.
FIG. 10. *B. plumosa* as above.
FIG. 11. *B. hypnoides* as above.
FIG. 12. *B. hypnoides* as above.

large portion of the plastid and was surrounded by plates of starch (Figs. 11, 12).

The observations of the pyrenoid number and plastid shape of *B. hypnoides* from dried material and of *B. pennata* from live material closely resembled the drawings made by Feldman (1937) for these species. Although it was difficult to ascertain the number of pyrenoids per plastid from dried material of *B. pennata,* this species could be distinguished from dried material of *B. plumosa* and *B. hypnoides* by the shape and size of the plastids, the proportion of the plastid occupied by the pyrenoid, and the nature of the starch granules around the pyrenoid. Caution about shape of the plastids in different portions of the macroalgal thallus should be born in mind when comparing dried material as plastid shape in live material of *B. pennata* was variable.

B. pennata grew as a dark green mat in the upper to mid-intertidal zone where on some granite rocks it had replaced *Enteromorpha* spp. as the dominant taxon.

SAN LUIS PASS

Dictyota dichotoma (Hud.) Lamour. Lowe and Cox (1978) reported a single drift collection of fragments of *D. dichotoma* from the grass beds at San Luis Pass at the west end of Galveston Island and commented that it may be more abundant in other years. In September 1979, *D. dichotoma* occurred in bloom proportions (one plant approximately every 10 cm) attached to the sediments and floating in the seagrass beds at San Luis Pass, but has not been collected since that time.

CHRISTMAS BAY

Gracilaria foliifera (Forsskål) Børg. Lowe and Cox (1978) also collected fragments of *G. foliifera* as drift in the grassbeds at San Luis Pass. *G. foliifera* occurred attached to oyster shells and other hard substrates in early Spring 1982 in this bay near San Luis Pass.

ROCKPORT-ARANSAS BAY

Acetabularia crenulata Lamour. Numbers of *A. crenulata* have steadily declined throughout the last eight years in the grassbeds of Aransas Bay near Rockport and in the ship basin at Rockport. At the time of the collections made by Edwards (1970, 1976) in this area, specimens of *Acetabularia* could be found every half to one meter apart (P. Edwards, personal communication). In late spring 1976, clusters of 3–4 plants of *Acetabularia* were found 10–20 meters apart. Isolated specimens of *Acetabularia* were collected in September, 1978, and none has been collected since in this study.

PORT ARANSAS JETTY

Bryocladia thyrsigera (J. Ag.) Schmitz. *B. thyrsigera* was listed by Edwards (1970, 1976) as rare. Since these collections began, *B. thyrsigera* has steadily increased in numbers and in the last six years has replaced *Bryocladia cuspidata* (J. Ag.) De Toni as an early colonizer on the jetty in the late spring. Its range extends throughout the intertidal zone. During the early summer it may comprise up to 60–70% of a square meter. The increased abundance of *B. thyrsigera* as compared to *B. cuspidata* can be seen in Fig. 1 of Kapraun's (1980) study of algal zonation on the Port Aransas Jetty, but he did not comment on the change in its abundance since Edwards' earlier study (1970, 1976) on the same jetty.

B. pennata Lamour. Specimens of *B. pennata* were collected in March 1982; no collections were made in 1983 or 1984 at Port Aransas.

Blue-Green Algal Layer. From 1978 to 1981 a blue-green algal layer, composed primarily of *Oscillatoria* spp. with occasional *Spirulina* trichomes appeared along the uppermost vegetation belt on the jetty in late winter and persisted until June. The entire spring-summer algal community, which in previous years had been prolific by May, did not become so until June. The appearance of *Centroceras clavulatum* (C. Ag.) Mont. was delayed until the blue-green algal layer diminished or disappeared.

PORT ISABEL

Sphacelaria rigidula Kütz. (= *furcigera* Kütz.). *S. rigidula,* reported from this area as *S. furcigera* by Humm and Hildebrand (1962) and by Conover (1964), was collected once in the fall of 1977 on the rocks under the Coast Guard Station (Baca, Sorensen and Cox 1979, their collection site III). Baca, Sorensen and Cox (1979) questioned its presence in this area because they did not collect the alga.

ACKNOWLEDGMENTS

I would like to thank the Marine Biology Department of Texas A&M University at Galveston for sponsoring the phycology field trips. Special acknowledgment is due Dr. L. O. Sorensen and Pan American University Marine Biology Laboratory at Port Isabel for their support in making these collections. R. J. Runnels provided the collections of *G. foliifera* from Christmas Bay and of *B. pennata* from Galveston in 1984. Drs. C. J. Dawes and D. Shevlin confirmed the identification of *B. pennata* and provided, along with Dr. J. W. LaClaire II, useful discussion on *Bryopsis.* Drs. E. R. Cox and G. A. Fryxell critically read the manuscript.

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VERTICAL DISTRIBUTION OF ZOOPLANKTON IN A SHALLOW TURBID ESTUARY

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ABSTRACT

Calcasieu Lake is a very shallow (< 2m), well-mixed estuary. Our objective was to determine whether selected zooplankton taxa aggregate near bottom during daytime in such a shallow turbid system. At three stations triplicate samples (one-minute tows) were taken first with a one-half meter net without towing bridle and then with an epibenthic pullsled. Data obtained from these two sampling strategies indicated a consistent trend of higher abundances of postlarval shrimps, fishes, decapods and copepods near bottom. Observed patterns of vertical distribution were taxa-specific. The observed stratification of zooplankton abundances may indicate biological responses associated with mechanisms of larval retention, diel migration, or demersal habits.

Accepted 6 March 1984

INTRODUCTION

Temporal changes in the distribution and abundance of many zooplankton taxa have been well documented in estuarine environments (Maurer, Watling, Lambert and Pembroke 1978; White, Heaton and Schmitz 1979; Christy and Stancyk 1982; Lambert and Epifanio 1982). The distributional pattern inferred for most species is diel migration, upward at dusk and downward at dawn, which results in higher zooplankton densities near the bottom of the water column during the day. Minello and Matthews (1981) demonstrated that even in very shallow estuaries significantly more zooplankton is collected at night than during the day. In order to attribute such differences to vertical migration rather than diel changes in avoidance, high concentrations must be demonstrated near bottom during the day. The purpose of our study was to identify vertical patterns of zooplankton abundance in a similar shallow estuary. Specifically, we wanted to determine whether selected zooplankton taxa aggregate near bottom during daytime in such a shallow turbid system.

MATERIALS AND METHODS

The study site, Calcasieu Lake (30°00′N latitude, 93°20′W longitude), covers approximately 255 km² and is the largest body of water in southwest Louisiana. It is part of a series of lakes connecting the Calcasieu River to the Gulf of Mexico. Previous characterization of the lake hydrography (Randall and James 1982) indicated no vertical physical discontinuities. The system is highly turbid with salinity decreasing up-estuary and to the east. The direction of net flow in the estuary is primarily influenced by tidal cycles; however, strong winds may override tidal flood or ebb resulting in longer than usual periods of outflow or inflow (Kelly, Randall and Schmitz 1982).

Monthly sampling was conducted during daytime high tide from May 1981 to April 1982 at three stations (Figure 1). Average high tide depth was 1.0–1.5 m for all stations. Weather

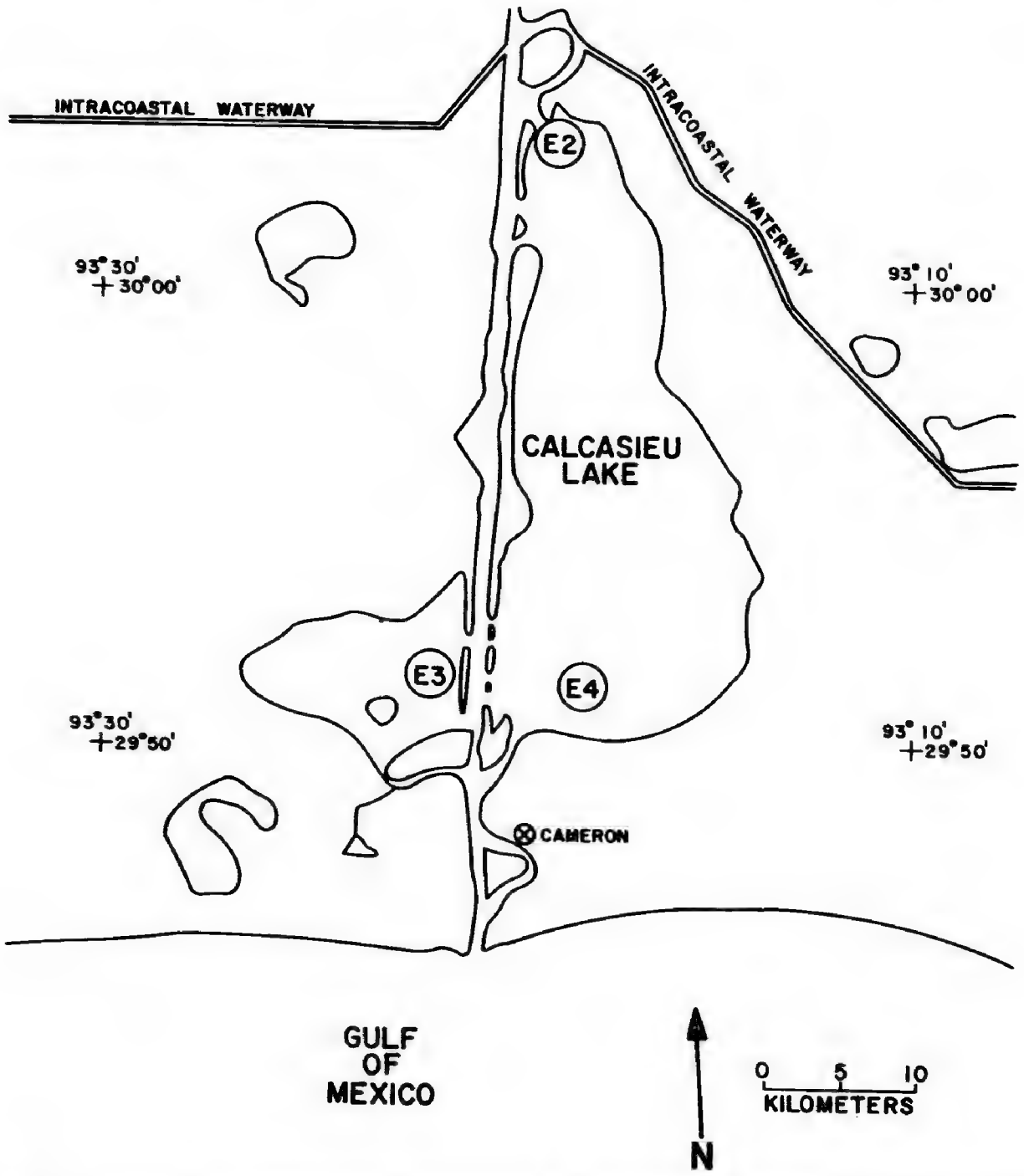

FIG. 1. Station numbers and locations for sampling Calcasieu Lake in southwestern Louisiana.

conditions were recorded at each station prior to sampling, and water quality was determined near surface and near bottom using a Hydrolab Series 8000 meter. Parameters measured

included pH, conductivity, dissolved oxygen and temperature. Water samples were collected near surface for nephelometric turbidity analysis.

At each station a triplicate series of one-minute tows was made at two depth strata, near-surface and near-bottom (boat speed of 1.5 knots). The upper level of the water column was sampled with a modified half-meter net (Figure 2) of 0.153 mm mesh netting and soft cod end.

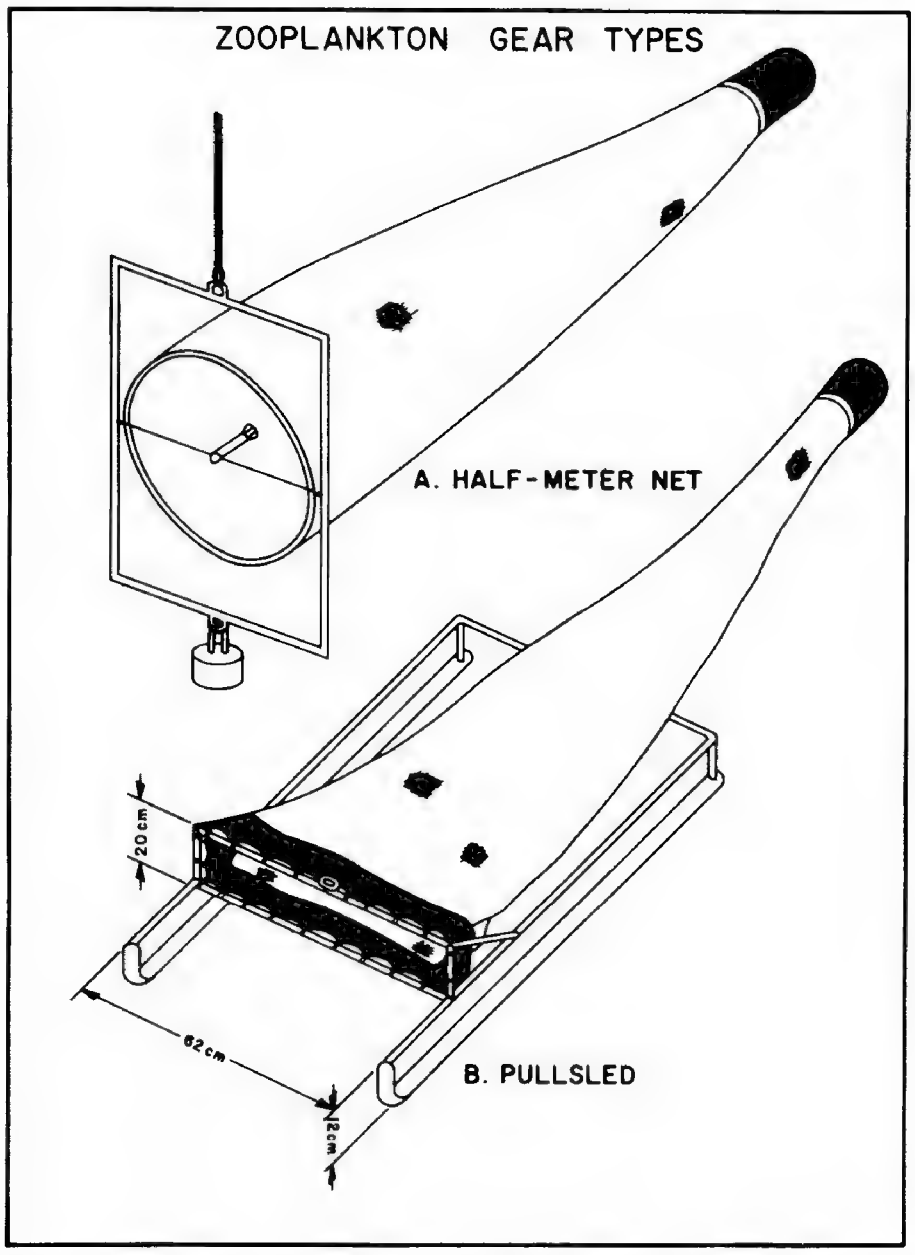

FIG. 2. Collection gear used in the estuary: A) half-meter net with swiveling steel frame and 14 kg depressor weight; B) pullsled with compressed mouth configuration. Both equipped with a 0.153 mm mesh Nitex net with soft cod end.

The circular ring was swivel-mounted inside a rectangular steel frame with a 14 kg depressor weight, which allowed the mouth of the net to remain perpendicular to the direction of tow. This gear was towed alongside a 6.7 m outboard craft with the mouth ring just below the surface. Near bottom (within 12 cm) samples were collected with a pullsled (Figure 2) rigged with a 0.153 mm mesh netting and soft cod end. This gear was quickly lowered from the stern while the boat was stationary to minimize surface contamination. The compressed mouth configuration (62 cm × 20 cm) allowed complete differentiation between the two depths sampled and provided a conservative population estimate relative to the half-meter net (Clutter and Anraku 1968). Whenever sediments were obvious in a pullsled sample, indicating contamination from the soft bottom, the sample was discarded and the tow repeated. The volume of filtered water was estimated from flowmeters that were located inside the mouth of each net. Filtration efficiency was optimized by combining brief tows with frequent net washing.

Samples were preserved in a 3–5% solution of formaldehyde in seawater buffered with sodium borate. All larval and postlarval fishes and postlarval shrimps were sorted from all samples. Except during the summer months, only the first sample of each replicate set was sorted for copepods and decapod zoeae. Copepods were removed from all samples during May 1981 through August 1981, and decapod zoeae were sorted from all replicates from May 1981 through July 1981. Subsampling was often necessary due to the high abundance of decapod zoeae and copepods; samples were split with a Folsom Plankton Splitter. The following groups were targeted for analysis due to their numerical dominance or commercial fishery importance: *Anchoa* spp., Gobiidae, *Penaeus* spp., *Uca* spp., *Rhithropanopeus harrisii*, *Acartia tonsa*, total fishes, total shrimps, total decapod zoeae, and total copepods.

Abundances were standardized to number of individuals per cubic meter of water filtered, and abundances of copepods and decapod zoeae were log transformed to moderate scalar differences due to wide abundance ranges. The non-parametric Wilcoxon Signed Rank Test (Mosteller and Rourke 1973) was chosen to test for significant differences in mean abundance values between the two gear types. Spearman's coefficient of rank correlation (Sokal and Rohlf 1981) was employed to test for association between turbidity and fish abundances. For both statistical procedures a one-tailed test was used. We used the coefficient of variability (standard deviation/mean) to examine relative variability between replicates.

RESULTS

PHYSICAL PARAMETERS

Comparisons of surface and bottom hydrographic values obtained in this study demonstrated no vertical stratification of pH, temperature, or dissolved oxygen. In general, the water column was isohaline from surface to bottom (Figure 3); however, salinity stratification was apparent at station E4 during November ($\Delta S = 3.3$ ppt) and December ($\Delta S = 5.5$ ppt) and at station E3 during February ($\Delta S = 6.2$ ppt). Turbidity values, which were highly variable between stations throughout the year, ranged from 2.5 NTU's to 120 NTU's (Figure 4).

FISHES

Mean abundances of total fishes fluctuated monthly with peak densities in May, August and September (Figure 5). According to the Wilcoxon test, total fishes were significantly more abundant in near-bottom samples (Table 1). A median coefficient of variation of 0.68 was calculated based upon twelve months of replicate data (Table 2).

Anchoa spp. and Gobiidae numerically dominated (17% and 48% respectively) the ichthyoplankton assemblage throughout the sampling period. The Wilcoxon test indicated significantly higher abundances of Gobiidae in the near-bottom samples; in contrast, abundances of *Anchoa* spp. were not significantly different between depth strata (Table 1). The median coefficients of variation for *Anchoa* spp. and Gobiidae were 0.48 and 0.59 respectively (Table 2). These values were based on data from the three months with highest abundances. Spearman's coefficient of rank correlation indicated that there were no significant associations between turbidity and either Gobiidae or *Anchoa* spp. abundances.

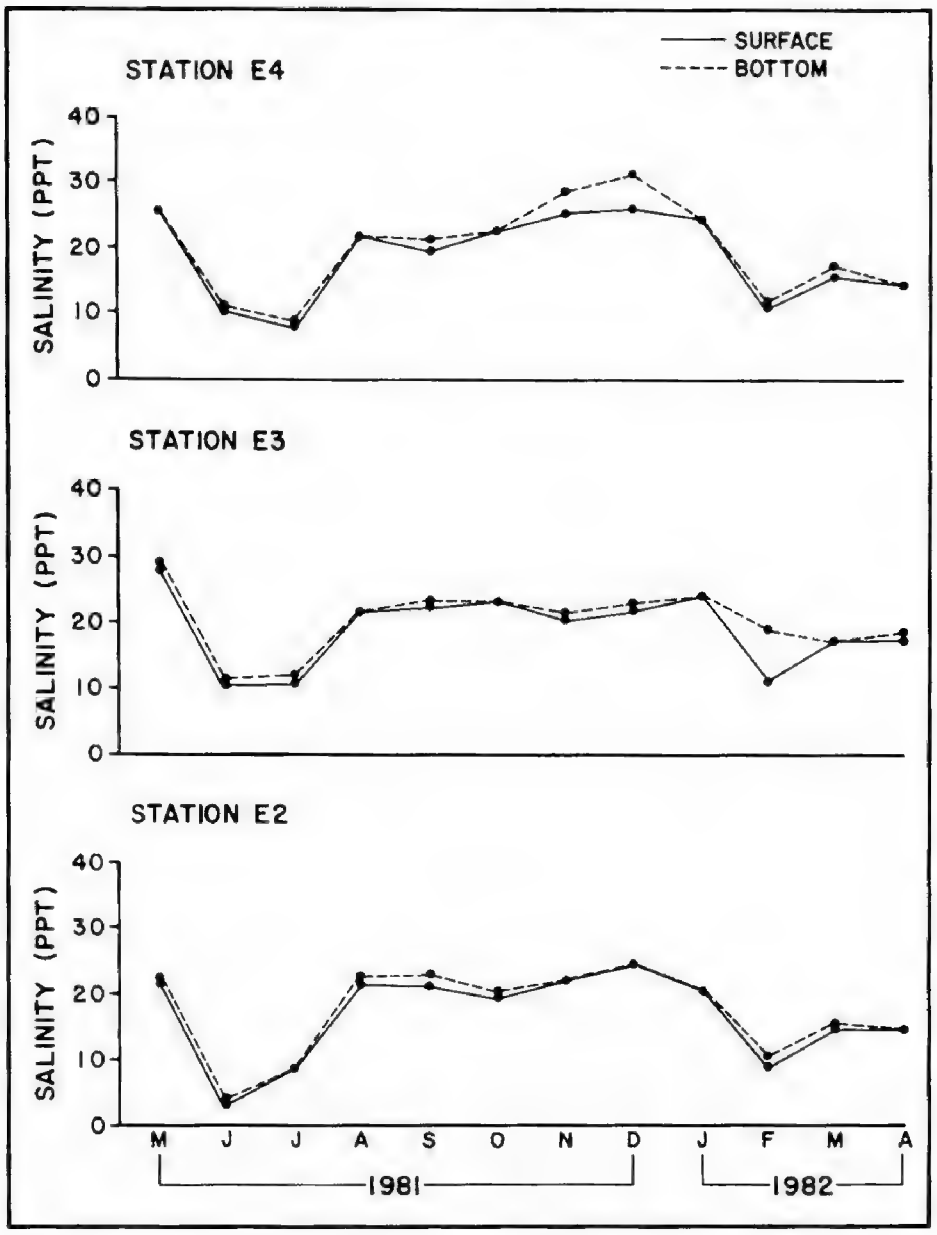

FIG. 3. Seasonal fluctuations in surface and bottom salinities (ppt) at each station for May 1981 through April 1982.

POSTLARVAL SHRIMPS

Mean total abundances of postlarval shrimps reached their highest densities during May, September and March (Figure 6). Based on the Wilcoxon test, total abundances of postlarval shrimps were significantly ($P < 0.001$) greater in the near-bottom stratum. A median coefficient of variation of 0.48 was calculated from the three months of highest shrimp abundances (Table 2).

Seven species of postlarval shrimps were captured during twelve months of sampling. Early postlarval *Penaeus* spp. was the dominant shrimp taxon January–April 1982, and comprised the largest percentage of the total annual shrimp catch (50%). The ratio of *Penaeus* spp. postlarvae collected near bottom to those collected near surface was 32:1.

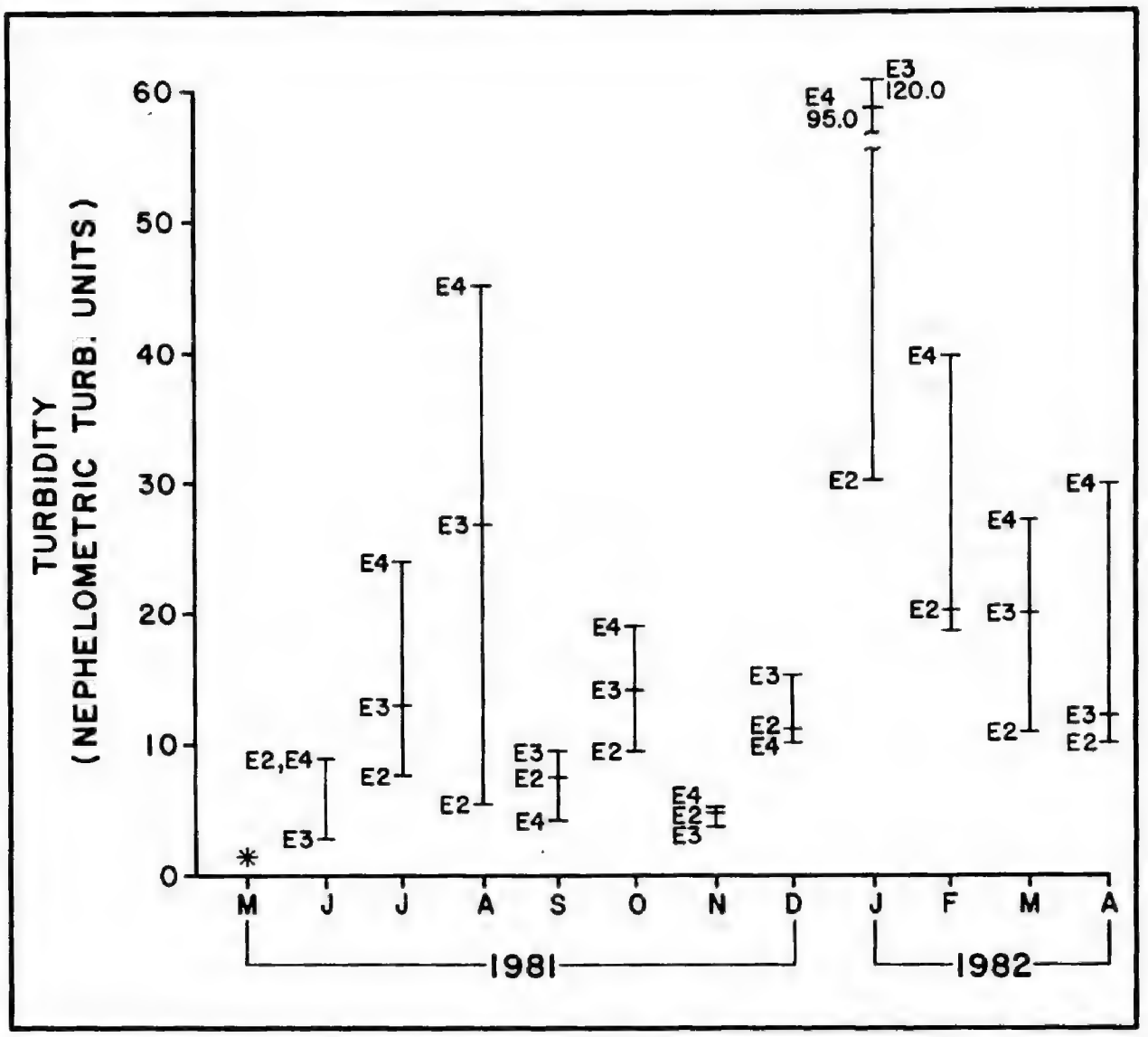

FIG. 4. Seasonal fluctuations in surface turbidities (NTU's) at each station for the 12 month study. * represents no data collected in May 1981.

DECAPOD LARVAE

Total abundances of decapod zoeae were greatest during the summer months, May–September (Figure 7). The Wilcoxon test indicated an overall pattern of significantly ($P < 0.05$) higher numbers of decapod zoeae in the near-bottom stratum (Table 1). For the three months for which we have replicate data the median coefficient of variation was 0.48 (Table 2).

Of the 21 species of decapod zoeae collected *Uca* spp. was numerically dominant (90% of total); *Rhithropanopeus harrisii* was the second most abundant species (3% of total). According to the Wilcoxon test, *Uca* spp. were captured in significantly ($P < 0.01$) greater numbers near bottom, whereas no significant difference between near-surface and near-bottom abundances were evident for *R. harrisii* (Table 1). Median coefficients of variation were 0.72 for *Uca* spp. and 0.77 for *R. harrisii* (Table 2).

COPEPODS

Copepods, which numerically dominated the zooplankton assemblage throughout this study, ranged from 10^2–10^6 individuals/m^3 (Figure 8).

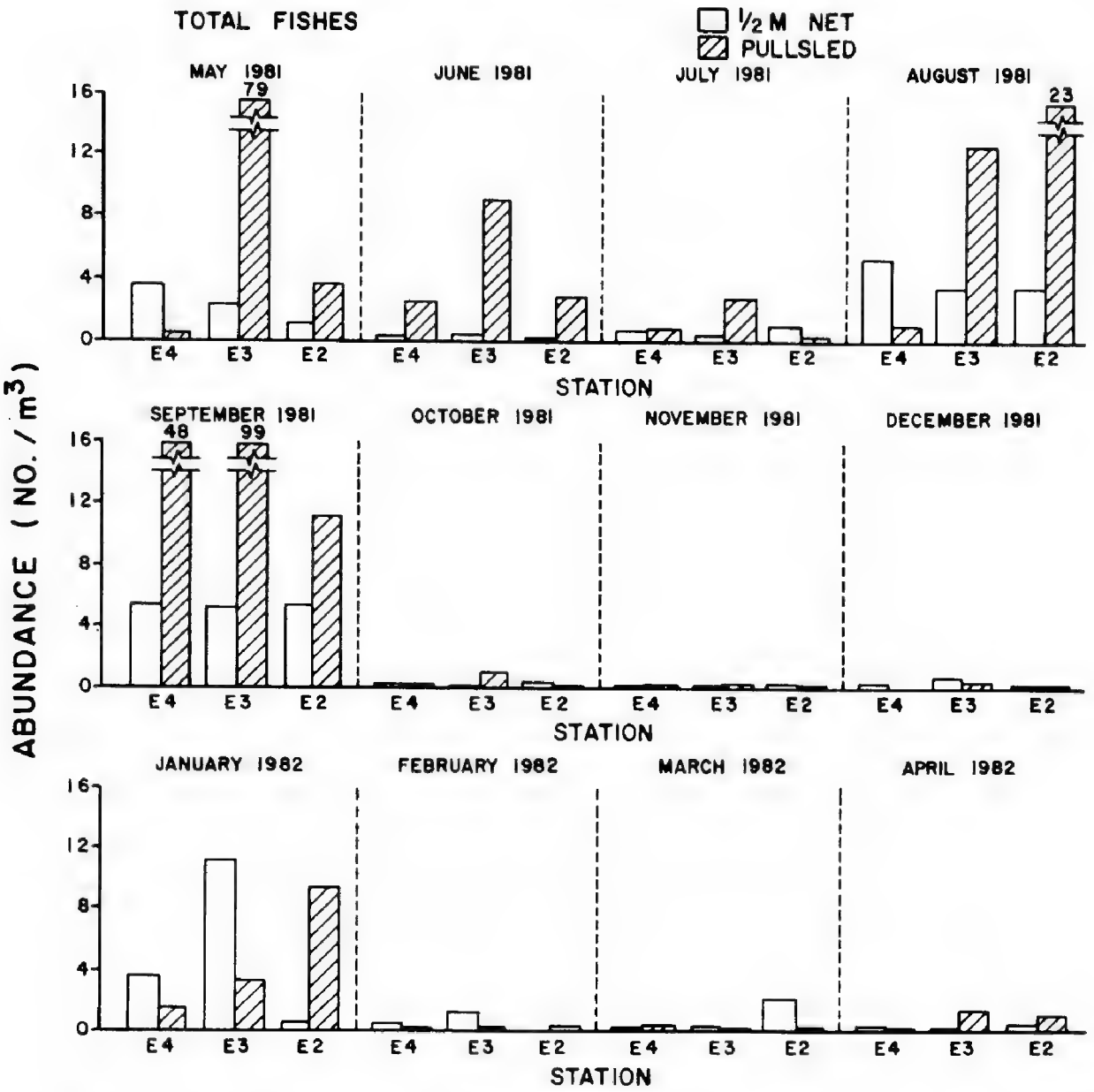

FIG. 5. Abundances of total fishes at each station for May 1981 through April 1982. Bars represent mean abundances based on three replicates for each gear type.

Acartia tonsa accounted for 90% of the total copepods collected in this study. The Wilcoxon test indicated that near bottom abundances of both copepodites and adults of *A. tonsa* were significantly ($P < 0.001$) greater than abundances observed for near-surface collections (Table 1). For the four months of replicate data available median coefficients of variation for *A. tonsa* adults and copepodites were 1.01 and 1.05 respectively (Table 2).

DISCUSSION AND CONCLUSIONS

Calcasieu Lake is a very shallow estuary with no vertical physical discontinuities. Comparisons of surface *versus* bottom hydrographic values obtained in this study indicated a generally isohaline water column with no vertical stratification of pH, temperature or dissolved oxygen. Despite the homogeneous physical nature of the water column, vertical patterns of zooplankton abundance were identified. Nonparametric analyses (Wilcoxon

TABLE 1

Summary of the results of the Wilcoxon Signed Rank Test for selected taxa. *P* values are based on paired comparisons of surface and bottom abundances at each station.

TAXA	W	TAXA	W
Total Fishes	**	*Anchoa* spp.	ns
Total PL Shrimps	***	Gobiidae	***
Total Decapod Zoeae	**	*A. tonsa* adults	***
Uca spp.	**	*A. tonsa* copepodites	***
R. harrisii	ns		

** $p < 0.01$
*** $p < 0.001$
ns not significant

TABLE 2

Median coefficients of variation for selected taxa based upon months with greatest abundances or when replicates were available. Means and standard deviations were calculated from raw data values.

TAXA	CV	TAXA	CV
Total Fishes	0.68	*Anchoa* spp.	0.48
Total PL Shrimps	0.48	Gobiidae	0.59
Total Decapod Zoeae	0.48	*A. tonsa* adults	1.01
Uca spp.	0.72	*A. tonsa* copepodites	1.05
R. harrisii	0.77		

test) of data over the entire study period indicated a long-term trend of significantly higher abundances of total fishes, shrimps, decapod zoeae and copepods in the near-bottom stratum. This stratification was apparent despite the conservative population estimate provided by the pullsled. Equal sampling efforts should demonstrate even greater abundances of these taxa near-bottom.

Vertical patterns of abundance were also identified for selected taxa. *Anchoa* spp. and Gobiidae were both abundant ichthyoplankton taxa, but they exhibited very different vertical distributions. Based on the Wilcoxon test, postlarval gobies were significantly more abundant near bottom, whereas anchovies were more uniformly distributed in the water column. The lack of correlation between turbidities and either anchovy or goby near-surface abundances indicates that avoidance of the half-meter net was not a serious problem. Early postlarval *Penaeus* spp. were more abundant near bottom, particularly in the spring when recruitment of shrimp into the estuary was at its peak. However, at this stage of development *Penaeus* spp.

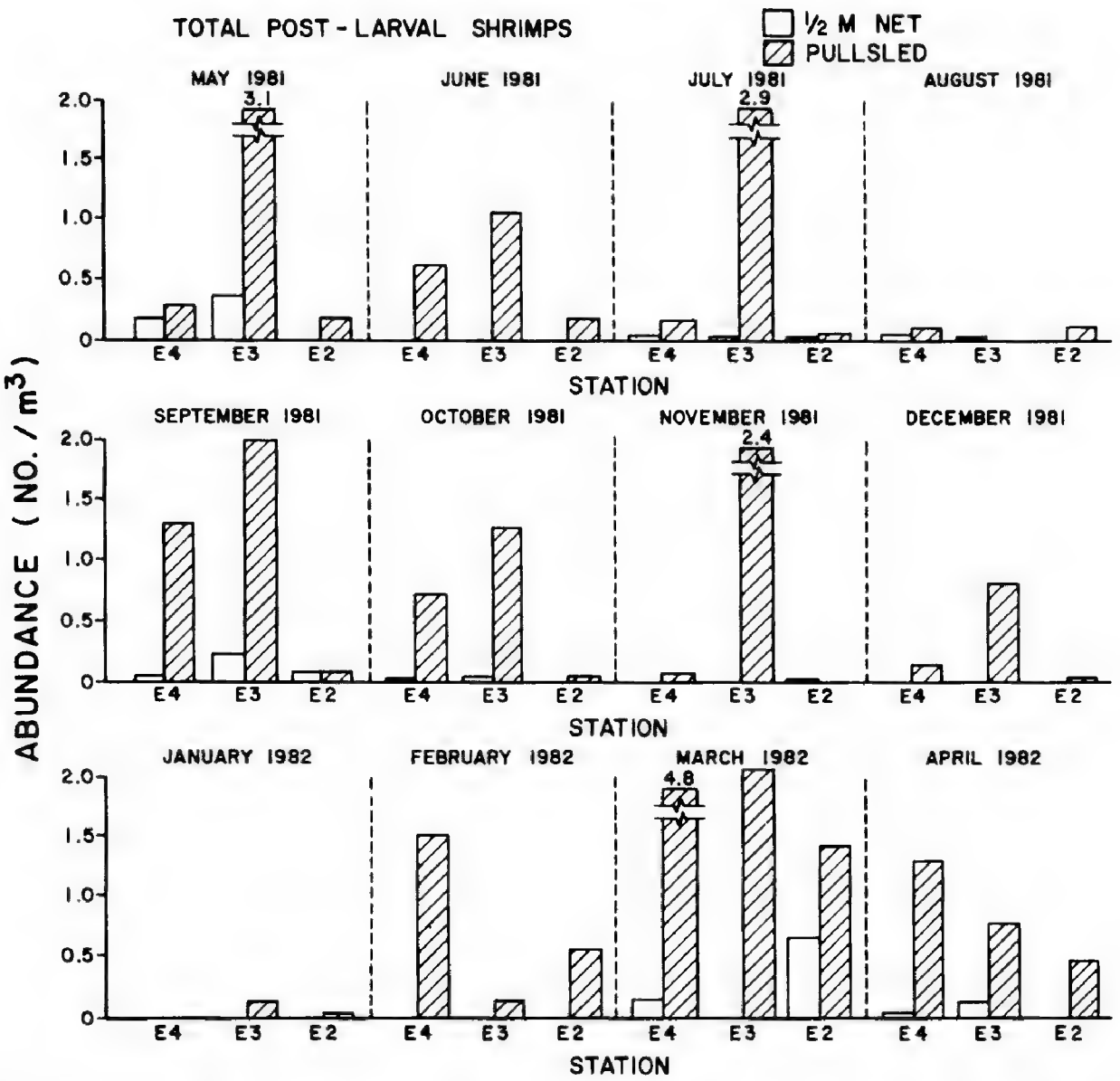

FIG. 6. Abundances of total postlarval shrimps at each station for the 12 month sampling period. Bars represent mean abundances based on three replicates for each gear type.

are changing from a planktonic to a demersal existence. *Uca* spp. dominated the decapod zoeae and were observed to aggregate in near-bottom waters of the upper Calcasieu estuary. The second most abundant decapod zoeae, *R. harrisii,* was also concentrated in the upper estuary as has been described for this species in other systems (Sandifer 1975, Cronin and Forward 1982). The vertical distribution of *R. harrisii* contrasted with that of *Uca* spp. in that the larvae of *R. harrisii* were not concentrated near bottom during our sampling. Significantly higher abundances of *A. tonsa* copepodites and adults occurred near bottom; however, their coefficients of variation (Table 2) indicate that *A. tonsa* was the only taxon which may aggregate into patches on our sampling scale.

Active vertical migration in response to tidal cycles has been described for zoeae of *R. harrisii* (Forward and Cronin 1980, Cronin and Forward 1982, Lambert and Epifanio 1982) as well as for larval herring (Graham 1972), postlarval spot and flounder (Weinstein, Weiss, Hodson and Gerry 1980), and larval and postlarval *Lucifer faxoni* (Woodmansee 1966). Estuarine diel migrations have been described for copepods (Maurer *et al.* 1978, White *et*

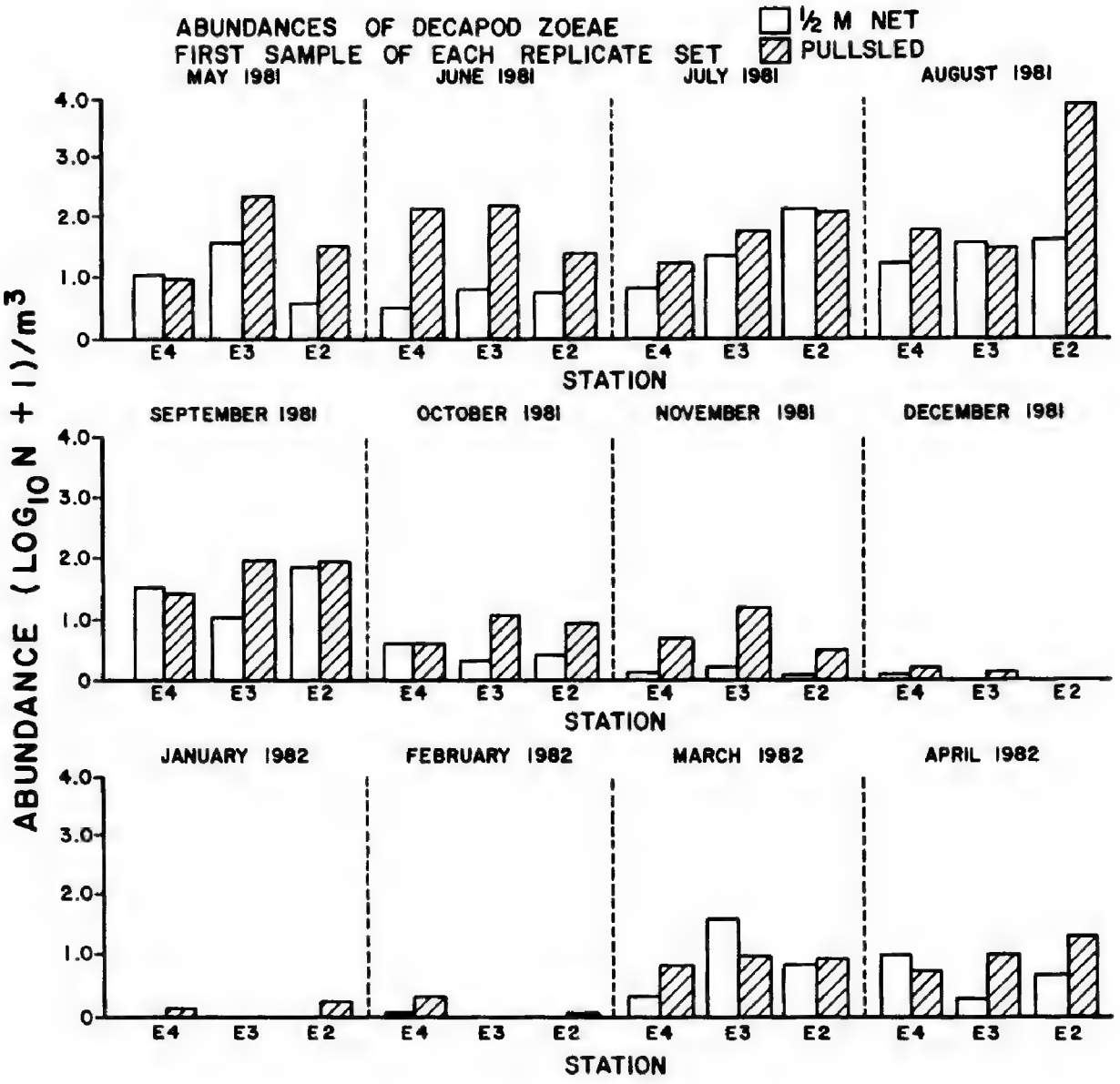

FIG. 7. Abundances of decapod zoeae at each station. Abundance values are log transformed and each bar represents the density of decapod zoeae in the first sample of each replicate set.

al. 1979) and *R. harrisii* (Sandifer 1975). Conversely, continuous accumulation near bottom has been described as a retention mechanism for zoeae of *Uca* spp. (Dittel and Epifanio 1982) and Atlantic croaker (Weinstein *et al.* 1980). These organisms do not migrate vertically but instead remain near bottom where net transport is landward.

Aggregation in bottom waters has been described as a means by which fishes and crustaceans maintain their resident populations in estuaries where net flow is seaward. In this study we have demonstrated that certain zooplankton taxa aggregate near bottom during the day in a very shallow, turbid estuarine system. Such patterns in vertical distribution may result from passive entrainment of individuals by water movement or may reflect an active orientation by the individuals to changing environmental conditions.

In summary, despite the homogeneous physical nature of the water column, vertical patterns of zooplankton abundance exist in the shallow Calcasieu estuary. This stratification of zooplankton abundance exist in the shallow Calcasieu estuary. This stratification of zooplankton taxa may

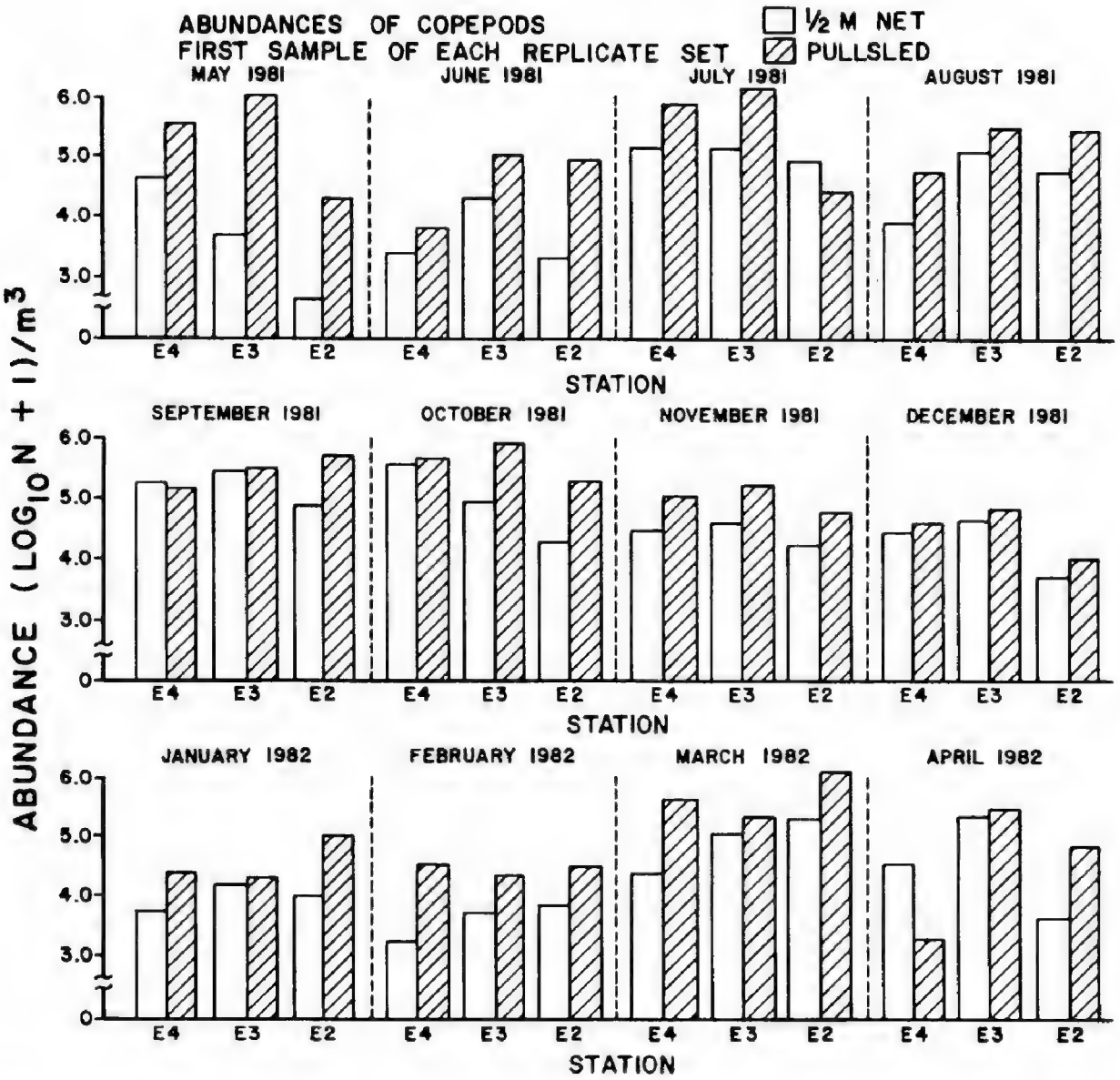

FIG. 8. Abundances of copepods at each station. Treatment same as Figure 7.

indicate 1) biological responses associated with mechanisms of larval retention; 2) diel migratory behavior; or 3) demersal habits exhibited by specific life-history stages of some taxa. More intensive investigation is necessary to distinguish among these possible explanations for the observed patterns of vertical distribution.

ACKNOWLEDGMENTS

We thank Don Weston for his valuable comments and Deanne Bonvillain and Terri Kirby for typing the manuscript. We also thank Dr. Tom Minello for his thorough review and valuable comments. Support for this work was provided by DOE Contract DE-AC96-80PO10228.

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HARD-BOTTOM MACROFAUNA OF THE EAST FLOWER GARDEN BRINE SEEP: IMPACT OF A LONG-TERM, SULFUROUS BRINE DISCHARGE

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ABSTRACT

A brine seep on the East Flower Garden Bank, northwest Gulf of Mexico, fills a small basin on the bank's southeastern flank at 72 m depth with anoxic, hypersaline (~200 ppt) water with a high total dissolved sulfide concentration (~1600 μg atoms/l) The brine is diluted by seawater as it flows down a 96-m long overflow canyon so that salinity and sulfide are at near-normal seawater concentrations at the canyon's mouth. Turbulent mixing above the brine stream and basin (lake) advects diluted brine to the adjacent hard bottom. Excluding the areas of full-strength brine, there is a significant increase in the number of hard-bottom invertebrates as one approaches the undiluted brine of the lake or the diluted brine of the canyon from the adjacent carbonate bank environment. Changes in taxonomic composition along this gradient are determined primarily by changing sulfide concentration and an increase in food supply. The data support the hypothesis that the brine seep system is a significant exporter of organic carbon and suggest that the normal hard-bank community at this depth may be food limited.

Accepted 27 February 1984

INTRODUCTION

The East Flower Garden Bank (EFGB) is a surface manifestation of an underlying salt diapir (Rezak and Bright 1981). Seawater percolating through the porous carbonate bank to the level of the salt dome produces brine seepage at several locations on the bank. One seep, located at 27°54′31.64″N, 93°34′53.27″W, has been described by Bright (1977), Bright, LaRock, Lauer, and Brooks (1980a) and Bright, Powell and Rezak (1980b). This seep forms a brine lake, Gollum's Lake, at 72 m depth in a basin near the southeastern edge of the EFGB. The brine lake overflows the basin at a sill to produce a brine stream that flows down a 96-m long canyon, Gollum's Canyon, before flowing onto the sandy bottom adjacent to the bank (Figure 1).

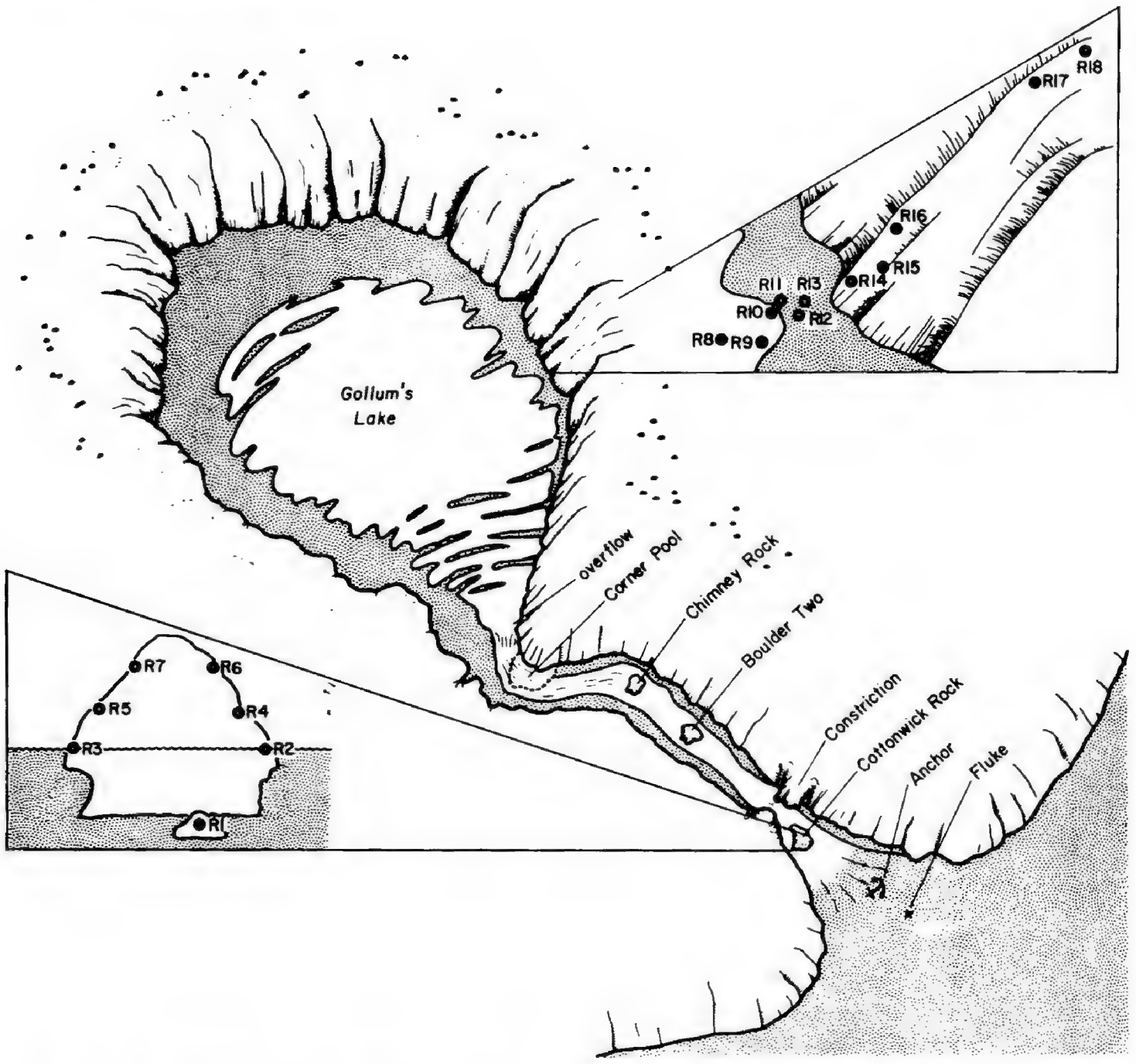

FIG. 1. Diagram of the East Flower Garden Brine Seep showing hard-bottom stations sampled during September, 1980.

Current speeds in the canyon's brine stream vary from 5 cm·sec^{-1} near the overflow to 25 cm·sec^{-1} at the canyon's mouth (Powell, Bright, Woods, and Gittings 1983). The residence time of the brine in the lake is estimated at 0.65 to 1.3 days (Rezak and Bright 1981) and, in the canyon, less than 15 min (Powell and Bright 1981).

Gollum's Lake is anoxic and has a high salt (200‰) and sulfide concentration (1600 μg atoms·1^{-1}) (Brooks, Bright, Bernard, and Schwab 1979; Powell *et al.* 1983). (The term sulfide will hereafter be used for total dissolved sulfide = $H_2S + HS^- + S^{-2}$.) The high density of the brine in Gollum's Lake and the relatively slow flow of brine through the lake inhibit mixing with the overlying seawater (Figure 2). The presence of 1–5 μg atoms·1^{-1} sulfide in the seawater overlying Gollum's Lake (Powell *et al.* 1983), however, suggests that some transport of brine across the lake-seawater interface

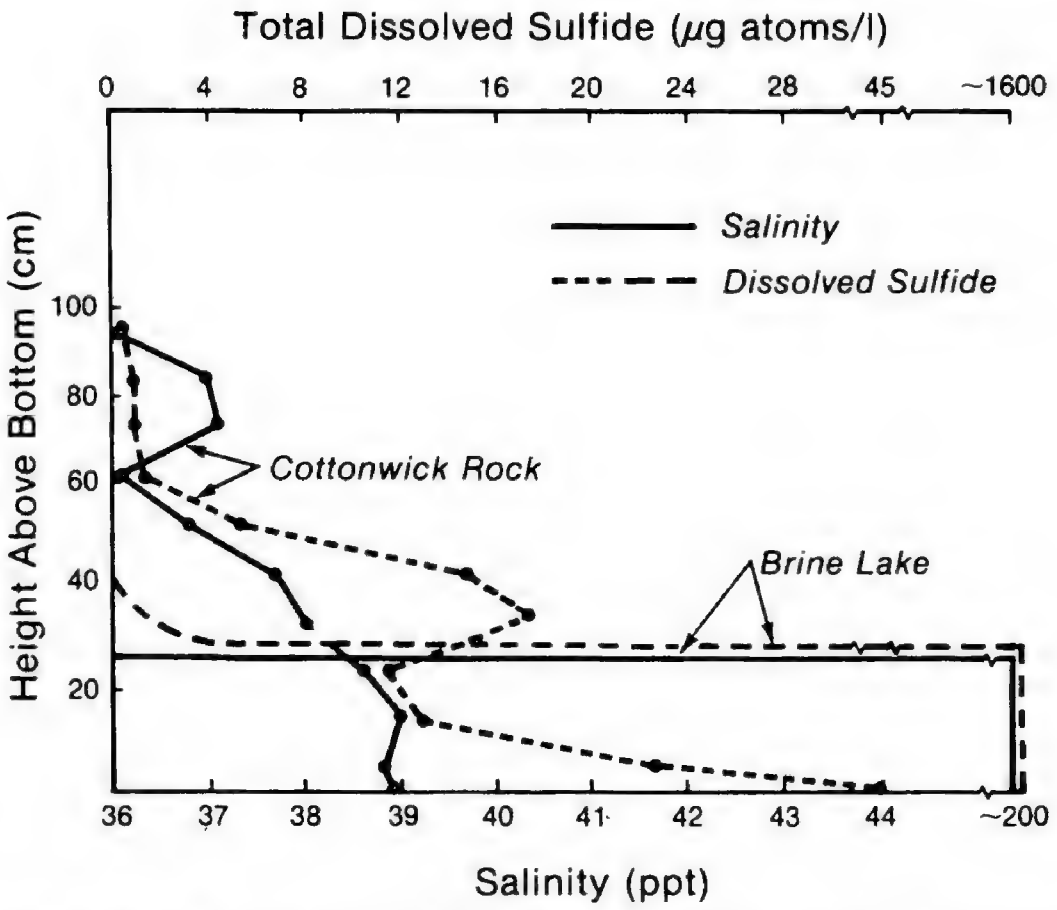

FIG. 2. Profiles of sulfide and salinity, both in the brine lake and along a vertical transect at the Cottonwick Rock. Data for Gollum's Lake are from Powell *et al.* (1983). Cottonwick Rock data came from two syringe arrays, one for salinity, one for sulfide, placed on the canyon bottom and triggered within 30 minutes of each other by lock-out divers. Within an array, all syringes were filled nearly simultaneously. Methods for analysis are given in Powell *et al.* (1983).

does occur. In contrast, in Gollum's Canyon, turbulent mixing by the gravity-driven flow of the brine stream down the canyon produces a more gradual and, vertically, more extensive salinity and sulfide gradient. Approximate bottom salinity and sulfide concentrations at Cottonwick Rock near the canyon mouth are 39‰ and 40 μg atoms·1^{-1}, respectively (Powell *et al.* 1983); sulfide is at detectable levels at least 1 m above the canyon floor (Figure 2).

The EFG brine seep is an example of a natural, long-term brine discharge. It provides the opportunity to study the long-term impact of increased salt and sulfide concentrations on the benthic biota of a deep-water reef. Both are of interest because (a) the impact of anthropogenically-produced brine on the benthic biota of the Gulf of Mexico has received increased attention with the development of strategic petroleum reserves (Bright *et al.* 1980b, Harper and McKinney 1980) and (b) the discovery of hydrothermal vent communities that subsist primarily on chemosynthetic sulfide oxidation (Ballard and Grassle 1979; Karl, Wirsen, and Jannasch 1980; Ruby, Wirsen, and Jannasch 1981) and the recent controversy about the existence of a thiobios (Reise and Ax 1979, Boaden 1980, Powell and Bright 1981) has heightened interest on the effects of sulfide on benthic communities.

The effect of the EFG brine seep on the community structure of the adjacent sandy bottom was described by Powell *et al.* (1983). Exclusive of the

brine lake and upper canyon, where both the salinity and sulfide content of the brine limited metazoan life, sulfide was the dominant parameter affecting benthic community structure. Sulfur bacteria and associated benthic microorganisms produced a white mat that covered the canyon floor from the overflow to downstream of Cottonwick Rock and at the lake's edge. Planktonic bacterial populations at the lake-seawater interface produced white sulfur flakes that were observed to float on the lake's "surface" (Lauer 1979; Bright *et al.* 1980a, b). Changes in sandy-bottom community structure included the numerical dominance of thiobiotic metazoans in the canyon (Powell and Bright 1981, Powell *et al.* 1983) and, below the mouth of the canyon, an increased abundance of oxybiota which was presumably caused by an increased food supply (Powell and Bright 1981).

Bright *et al.* (1980b) divided the biotopes of the EFGB hard bottom into two primary zones, a bank-top coral reef at 15–52 m depth and a deeper-water algal-sponge zone at 45–82 m depth. The substrate of the algal-sponge zone consisted of coralline algal nodules and consolidated reefrock interspersed with sandy patches. The majority of studies on the invertebrate fauna of carbonate reefs dealt with the shallow portions of coral reefs (*e.g.*, McCloskey 1970; Brander, McLeod, and Humphreys 1971; Brock and Brock 1977). A relatively small body of knowledge exists for the infauna associated with deep-water, carbonate-reef communities such as those of the algal-sponge zone at the EFGB (Abbott 1975, Hogg 1975). The study reported herein focused on the macrofauna of the algal-sponge zone adjacent to Gollum's Lake and Canyon with the purpose of describing the effect of both the increased sulfide concentration and the increased food supply on the biota of the deep-water reef.

METHODS

Coralline algal nodules and consolidated reefrock were collected by lock-out divers and by a hydraulic manipulator arm using the *Johnson Sea-Link* submersible in September, 1980. Eighteen stations were sampled along two transects (Figure 1). Single algal nodules or portions of consolidated reefrock were collected at each station. The transect located on the east edge of Gollum's Lake comprised 11 stations (R8–R18). Samples at stations R8 and R9 yielded nodules which were completely submerged in the brine lake. Stations R10 and R11 were located at the "shoreline" of Gollum's Lake and consisted of one large nodule which was subsequently divided for sampling purposes to separate the portion submerged in Gollum's Lake (R10) from the portion above the lake-seawater interface (R11). Stations R12 and R13 yielded two samples taken from a large bi-lobed nodule located on the thin sandy "beach" separating the brine lake from the surrounding bank (see Figure 1). R12 was partially covered by the sandy sediment so that interstitial brine, if present in the sediment surrounding the lake, may have influenced the macrofauna collected with it; R13 was entirely above the sediment surface. Stations R14–R18 provided samples of consolidated reefrock broken off the hard bank. R14–R16 and R17–R18 can be considered two sets of replicate samples. R14 was collected 0.4 m from the "shoreline" of the brine lake; R15 and R16 were both collected within 0.6 m from the shoreline. Stations R17 and R18 yielded control samples from the surrounding bank area at approximately 70.7 and 68.9 m depth, respectively.

The second transect, comprising seven stations, was located along a vertical portion of Cottonwick Rock near the mouth of Gollum's Canyon (Figure 1) at 78.1 m. The rock, called

Cottonwick Rock due to a large school of Cottonwick fish (*Haemulon melanurum*) that frequented the location, extended upward to a depth of approximately 76 m. The sample from R1 was a nodule collected from the brine stream bed immediately adjacent to Cottonwick Rock. Stations R2 and R3 were intended to be replicates from the same level on Cottonwick Rock, approximately 0.3 m above the stream bed. Similarly, replicate stations R4 and R5 were located approximately 1.0 m from the bottom and replicate stations R6 and R7 were located at the top of Cottonwick Rock, about 2.0 m from the bottom. In each case (R2–R7), chunks of reefrock were collected. R2 and R3 were immediately above a marked change in coloration of Cottonwick Rock. Below these stations, the rock was whitish in appearance, similar to the canyon floor and station R1, presumably due to a mat of sulfur bacteria extending from the canyon floor up onto the rock.

All samples were preserved in 5% formalin. In the laboratory, any sediment associated with the rock was removed by a gentle flushing with 5% formalin and was stained with Rose Bengal in 5% formalin. The rocks were subsampled to obtain samples ranging from approximately 20–200 g. These subsamples were weighed, displacement volumes obtained and exposed surface areas (*i.e.* non-sectioned surface area) estimated. Each subsample was examined preliminarily to remove calcareous organisms such as pelecypods and to note the areal coverage of encrusting organisms.

The most significant problem associated with estimating abundances of hard-bottom infauna has been extraction. Procedures for extraction of infauna from calcium carbonate rock include chipping the rock apart (McCloskey 1970, Kohn, and Lloyd 1973; Hutchings 1974), driving the infauna out of the rock by imposing anoxia (Leviten 1976), or dissolving the calcium carbonate portion of the rock, which leaves behind an organic matrix containing the preserved organisms (Brock and Brock 1977). A modification of the latter technique was used here. The rock samples were submerged independently in a commecially distributed decalcifying solution commonly used in histological procedures. The decalcifying solution contained 0.7 g/l EDTA tetrasodium salt, 8 mg/l sodium potassium tartrate, 99.2 ml/l HCl and 0.14 g/l sodium tartrate. Frequent changes of the solution were made over the 24–48-hour period it took for total dissolution. The organic portions left after dissolution were preserved in 5% formalin containing Rose Bengal stain.

The macrofauna (>0.5mm) were sorted from each sample and identified. Presence or absence was noted for meiofaunal groups and groups where direct counts were not feasible (*e.g.* Protozoa, Porifera, Nematoda, and Copepoda). Numerical abundances were standardized to numbers per 100 g of rock, numbers per 100 ml of rock and numbers per square meter of rock surface. The numbers per square meter standardization was chosen for subsequent analyses because the population maxima for the majority of the enumerated taxa occurred near the surface of each nodule (*i.e.* within approximately 3 cm of the surface). The other standardizations gave population estimates that were more biased by variations in the amount of interior volume of each sample that was analyzed. The samples' surface areas averaged approximately 0.03 m^2. For typical sample counts, therefore, the tabulated values may be divided by approximately 33.

Cluster analysis was performed using Euclidean distance as the similarity index after log-transformation of the data. An agglomerative hierarchical type clustering method available from the Statistical Analysis Sytem (SAS) program package was employed.

RESULTS

The numerical abundances of the enumerated taxa from the 18 stations sampled along both transects are summarized in Tables 1 and 2. Control stations R17 and R18 probably are representative of the biotic composition of the algal-sponge zone at the EFGB. The dominant groups are sipunculans and annelids at both stations. The annelids are characterized by a preponderance of one family, Syllidae. Total abundances are 5000–15000 organ-

TABLE 1

Invertebrate abundances in numbers per square meter at 18 stations around the East Flower Garden brine seep: (–) indicates no individuals collected; (×) indicates individuals collected but not enumerated.

	STATION																	
	R1	R2	R3	R4	R5	R6	R7	R8	R9	R10	R11	R12	R13	R14	R15	R16	R17	R18
Protozoa	-	x	x	-	x	-	-	-	-	-	x	-	x	x	x	x	x	x
Porifera	-	x	x	x	x	x	x	-	-	-	x	x	x	x	x	x	x	-
Cnidaria																		
Scyphozoa	-	6087	1700	4020	1730	2260	1372	-	-	-	3208	810	-	960	2566	4240	280	264
Anthozoa	-	307	-	-	-	187	1875	-	-	-	-	-	-	-	-	-	-	-
Nemertea	x	x	-	-	-	-	-	-	-	-	-	x	x	-	-	x	-	-
Aschelminthes																		
Nematoda	x	x	x	x	x	x	-	-	-	-	x	x	x	x	x	x	x	x
Ectoprocta	-	-	-	-	x	x	x	-	-	-	-	-	-	-	-	x	-	x
Annelida	20786	22421	20591	12272	32089	16737	23031	-	-	-	17334	18962	46330	8482	6757	20510	6725	3034
Mollusca																		
Polyplacophora	-	-	-	457	765	367	1244	-	-	-	292	-	-	110	-	80	110	77
Gastropoda	1780	-	-	-	430	300	122	-	-	-	125	-	20	220	32	160	70	14
Bivalvia	-	353	-	327	750	603	1869	-	-	-	42	-	1310	420	100	130	340	125
Sipuncula	167	2037	1870	6287	3170	5403	7241	-	-	-	17917	11080	8440	5677	1391	2020	4900	2057
Arthropoda																		
Copepoda	x	x	x	x	x	x	x	-	-	-	x	x	x	x	x	x	x	x
Ostracoda	x	x	x	x	x	x	x	-	-	-	x	-	x	-	x	x	x	x
Cumacea	-	-	-	-	-	-	-	-	-	-	x	-	x	-	-	-	-	-
Tanaidacea	21457	45943	16100	8270	7755	90	1098	-	-	-	10333	135	90	-	732	810	430	71
Amphipoda	17930	4010	3670	647	2155	730	976	-	-	-	3000	-	615	330	113	220	140	29
Isopoda	3477	59597	42800	14760	15125	7753	8064	-	-	-	1917	945	1925	1597	1829	2970	230	-
Decapoda	-	20	-	-	-	-	-	-	-	-	125	-	20	-	-	30	-	-
Echinodermata																		
Echinoidea	-	-	-	-	-	-	625	-	-	-	-	-	-	-	-	-	23	-
Ophiuroidea	-	110	-	133	-	-	-	-	-	-	-	135	455	220	-	-	23	163
Holothuroidea	-	-	-	-	-	187	-	-	-	-	-	-	130	110	-	-	120	-
Asteroidea	-	-	-	-	-	90	-	-	-	-	-	-	20	-	-	-	230	-
Chaetognatha	-	-	-	-	-	180	244	-	-	-	-	-	-	110	-	-	-	-
Pisces	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-
TOTAL	65567	140885	86731	47173	63969	34887	47761	0	0	0	54293	32067	59355	18236	13520	31170	13611	5687

isms per m^2 which is roughly equivalent to the 8000–20000 per m^2 reported from the adjacent sandy-bottom control stations by Powell *et al.* (1983). (The numbers probably are nearly equivalent in so far as the Powell *et al.* (1983) data over-estimated abundances of comparable taxa because individuals of meiofaunal size were included.) Compared to most other stations on either transect, however, both control stations had the lowest total abundances and the lowest abundances for most individual taxa.

Substantial changes occurred in both faunal composition and faunal abundance in and adjacent to the EFG brine seep system (Figures 3, 4, 5, 6). No living metazoans were found at stations R8, R9 and R10, located within the brine lake. Further discussion will exclude reference to these stations. On both transects, a Cox-Stuart test for trends (Conover 1980) showed a significant downward trend in total abundance with increasing distance from the lake or canyon floor (Table 3). For example, the abundances of tanaidaceans, amphipods and cirratulid polychaetes decreased significantly with distance from the canyon floor on the Cottonwick Rock transect (Figures 5 and 6). Exclusive of the lowermost station (R1), isopods, tanaidaceans, and scyphozoans had the lowest average numbers at the replicate stations R6, R7 located highest above the canyon floor (Figures 5 and 6). Numbers of polyplacophorans, bivalves, sipunculans, dorvilleids and

TABLE 2

Annelid group abundances in number per square meter at the 18 brine seep stations.

	R1	R2	R3	R4	R5	R6	R7	R8	R9	R10	R11	R12	R13	R14	R15	R16	R17	R18
Ampharetidae	-	-	-	-	-	-	-	-	-	-	-	406	872	-	100	304	-	-
Amphinomidae	-			-	333	-	-	-	-	-	-	-	454	-	-	78	23	-
Capitellidae	-	523	200	1123	1616	-	-	-	-	-	-	968	539	-	-	547	474	-
Chaetopteridae	-	8942	-	133	6833	-	-	-	-	-	-	-	-	-	-	-	-	-
Chrysopetalidae	-	135	-	231	217	878	488	-	-	-	292	135	784	872	315	339	331	139
Cirratulidae	1208	873	1149	64	666	185	1000	-	-	-	583	406	7806	108	341	464	522	-
Dorvilleidae	187	340	200	649	8946	2463	488	-	-	-	333	135	680	323	125	200	159	250
Eunicidae	333	3236	4272	600	2050	583	2250	-	-	-	1167	406	330	530	266	251	278	14
Glyceridae	-	45	-	-	416	-	-	-	-	-	-	135	-	115	16	-	-	-
Hesionidae	-	90	-	-	416	276	-	-	-	-	-	-	556	-	386	1316	-	188
Lumbrineridae	353	750	-	596	334	370	1000	-	-	-	-	1081	-	226	-	170	76	-
Maldanidae	167	45	1543	1297	-	217	-	-	-	-	1333	4460	872	-	-	-	79	362
Nereidae	12914	-	200	64	1652	610	3488	-	-	-	1125	406	820	968	132	347	423	76
Opheliidae	-	687	299	1097	1083	870	-	-	-	-	-	-	244	-	-	943	261	-
Paraonidae	-	167	-	-	-	-	-	-	-	-	-	-	-	-	-	78	-	-
Phyllodocidae	-	23	-	167	-	167	-	-	-	-	500	270	-	223	-	-	-	-
?Questidae	542	-	-	333	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sabellariidae	-	-	-	-	217	-	-	-	-	-	-	-	-	-	-	-	-	-
Sabellidae	-	83	1570	191	634	370	-	-	-	-	5417	832	1254	541	16	740	99	129
Serpulidae	-	2735	75	-	-	-	122	-	-	-	42	-	1730	108	-	26	326	-
Sphaerodoridae	-	417	-	-	666	-	-	-	-	-	-	-	208	-	16	185	79	-
Spionidae	167	3202	1522	527	1087	91	625	-	-	-	1917	2184	2092	430	125	147	175	389
Syllidae	2082	125	7364	4807	6906	8903	13507	-	-	-	2000	5855	23430	3374	4319	10924	2847	1507
Terebellidae	-			393	-	537	-	-	-	-	-	833	680	230	600	118	450	-
Oligochaeta	2833	-	2197		-	-	-	-	-	-	2125	428	2195	434	-	3333	123	-
Polychaete(?)	-	-	-	-	217	217	-	-	-	-	500	22	784	-	-	-	-	-
Total	20786	22421	20591	12272	32089	16737	23031	0	0	0	17334	18962	46330	8682	6757	20510	6725	3054

syllids increased significantly with distance above the canyon floor, but the abundance of these taxa did not increase enough to prevent the uppermost Cottonwick Rock stations (R6, R7) from having the lowest total abundances on the transect. Even so, both total numbers and the abundances of most of the individual taxa at R6 and R7 were substantially above control levels (R17, R18) and many of the intermediate lake transect stations (R12–R16). Similarly, on the Gollum's Lake transect, a Cox-Stuart test for trends (Table 3) indicated that sipunculan numbers decreased significantly with distance from Gollum's Lake, as did the abundances of polychaetes in the families Eunicidae, Nereidae, Sabellidae and Spionidae. The numerically dominant polychaete family (Syllidae) at these stations showed no trend at all, however. In general, those taxa whose greatest relative abundance (percent of total fauna collected) occurred at the intermediate stations of the lake transect (R12–R16), such scyphozoans and isopods, tended to be most abundant on the middle Cottonwick Rock stations. Those taxa whose relative abundances were at least as high at the control stations (R17, R18) as elsewhere on the transect, such as sipunculans and molluscs, tended to have highest numbers at the uppermost Cottonwick Rock stations (R6, R7).

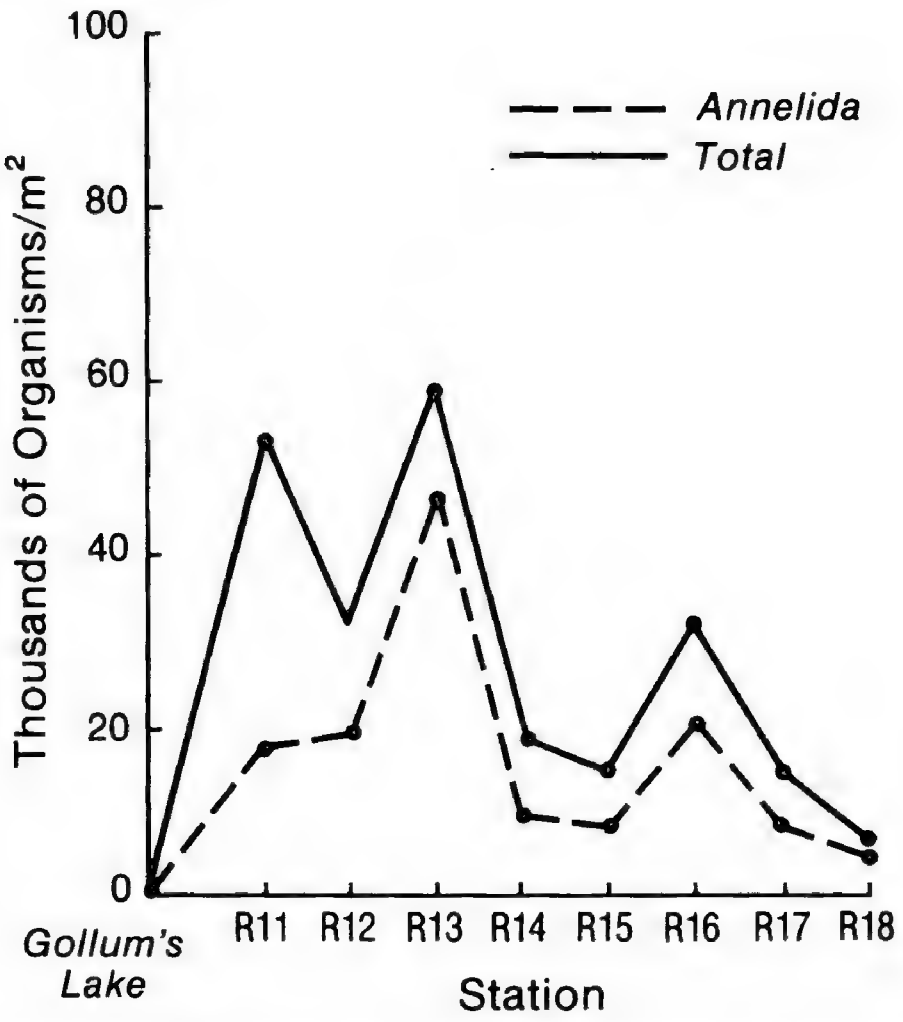

FIG. 3. Abundances of Annelida and total abundances at stations along the brine lake transect.

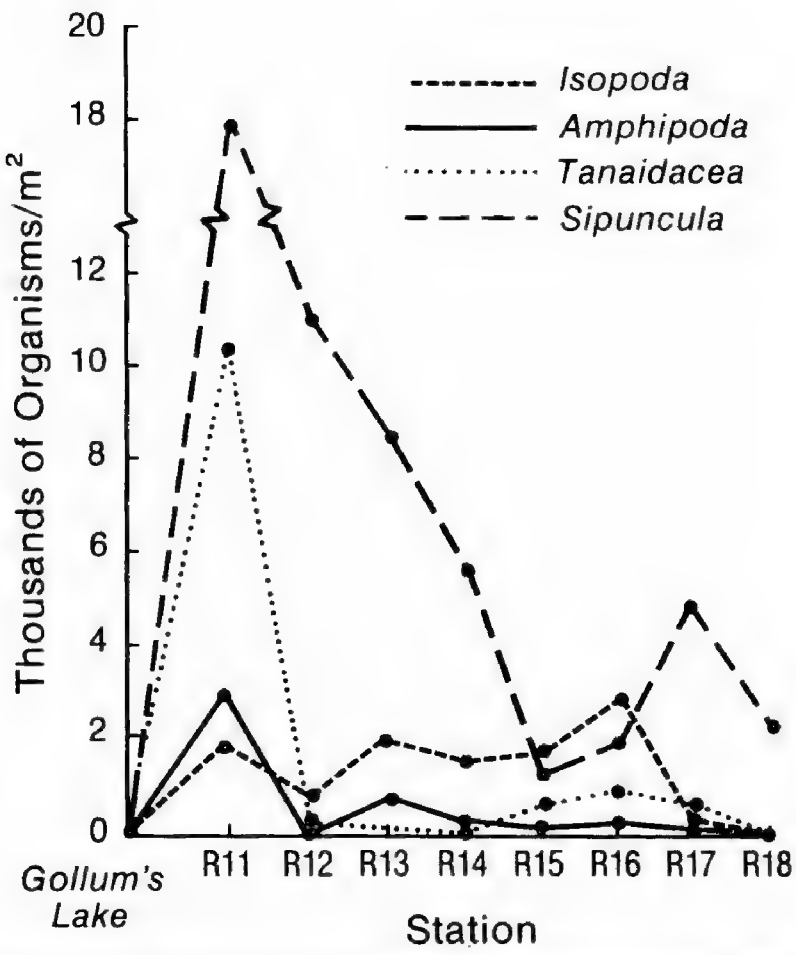

FIG. 4. Abundances of selected taxa at stations along the brine lake transect.

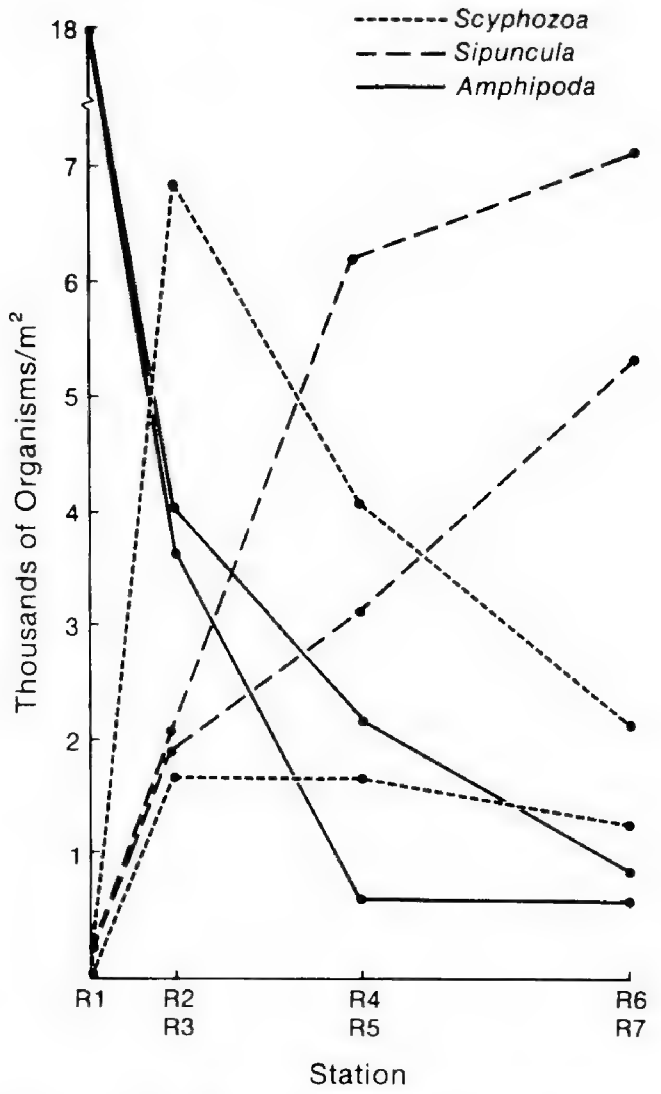

FIG. 5. Abundances of selected taxa, and total faunal abundance at stations along the Cottonwick Rock transect. Stations on x-axis are spaced according to relative distance from one another in the vertical dimension. Double-line curves indicate ranges of values obtained in replicate samples.

Among the annelids, those taxa with significant decreases in abundance with increasing distance from Gollum's Lake along the lake transect were all present in highest numbers at the lowermost stations of the Cottonwick Rock transect (R1, R2 or R3). Exclusive of R1, stations near the brine lake or canyon floor (R2, R3, R11) had in common the importance of tube-dwelling filter feeders: sabellids and spionids at R3 and R11, and chaetopterids, serpulids and spionids at R2. The deposit-feeding taxa, Maldanidae and Oligochaeta, were numerically more important near the brine source (*i.e.* the brine lake or canyon floor) on either transect. In contrast, Capitellidae and Ampharetidae had higher abundances at the intermediate lake transect stations and, for Capitellidae at the middle Cottonwick Rock stations. Syllid peak abundances also were found at the intermediate lake transect stations (R13, R16) and the two upper Cottonwick Rock stations (R6, R7).

On both transects, the station nearest the brine source (R1, R11) was distinctly different in taxonomic composition from the others. At station R11 at the edge of the lake, for example, annelids were relatively uncommon considering the high total number of organisms collected, whereas sipunculans, tanaidaceans, and amphipods were present in much higher than usual

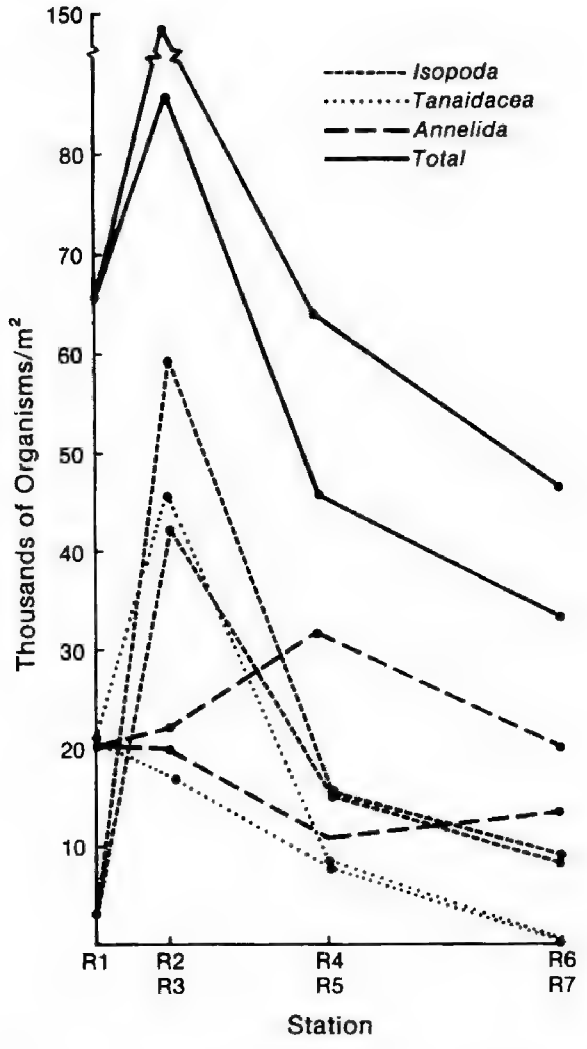

FIG. 6. Abundances of selected taxa at stations along the Cottonwick Rock transect. Stations on x-axis are spaced according to relative distance from one another in the vertical dimension. Double-line curves indicate range of values obtained in replicate samples.

TABLE 3

Results of Cox-Stuart Test for Trends for individual transects. Direction along each transect is from the brine source to the most control-like stations (R17, R18 or R6, R7). Due to limited degrees of freedom, the lowest achievable level of significance on the Cottonwick Rock transect is $\alpha = 0.125$ ($d.f. = 3$); on the lake transect trends are reported at $\alpha = 0.0625$ ($d.f. = 4$).

Cottonwick Rock transect		Brine Lake transect	
Parameter	Trend	Parameter	Trend
Major groups:		Major Groups:	
Polyplacophora	upward	Sipuncula	downward
Bivalvia	upward	Total numbers	downward
Sipuncula	upward		
Tanaidacea	downward		
Amphipoda	downward		
Total numbers	downward		
Polychaetes:		Polychaetes:	
Cirratulidae	downward	Eunicidae	downward
Dorvilleidae	upward	Nereidae	downward
Syllidae	upward	Sabellidae	downward
		Spionidae	downward

numbers. Among the annelids, the eunicids, nereids, spionids, sabellids and oligochaetes were present in higher relative abundance at R11 than at most other lake transect stations, whereas the syllids were poorly represented. Similarly, the station nearest the canyon floor, R1, was characterized by extremely high numbers of amphipods and relatively high numbers of tanaidaceans and nereid polychaetes. Nereids were more abundant at station R1 than at any other station and represented 62% of the annelid fraction. In addition, oligochaetes were more abundant (14% of the annelids) than at most stations, whereas syllids were present in unusually low numbers (10% of the annelids).

Similarities observed in the faunal compositions of the two transects were supported by the cluster analysis (Figure 7). Station R11 at the lake end of

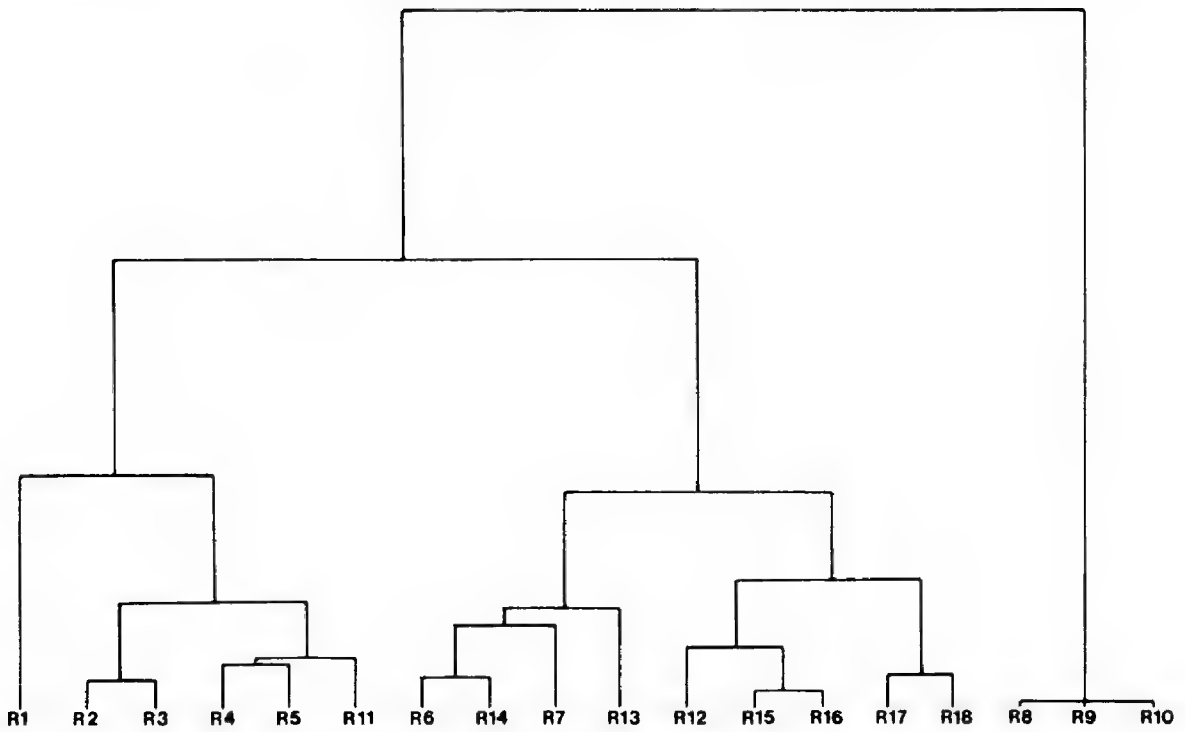

FIG. 7. Results of cluster analysis on the numerical abundance data in Table 1.

the lake transect clustered with the middle stations of the Cottonwick Rock transect (R2–R5) and not with stations in closer proximity. Station R1 on the canyon floor was more similar to this group of stations than to the others. The remaining lake transect stations fell into two similar groups. Two of the stations adjacent to R11 (R13, R14) near the shoreline of Gollum's Lake clustered with stations R6 and R7 from the top of Cottonwick Rock. The other stations (R12, R15, R16) formed a second cluster which included the two control stations R17 and R18. Thus, the change in faunal composition along the two transects was similar. Furthermore, the shift in faunal composition that occurred over the entire Cottonwick Rock transect which ended 2 m above the canyon floor, corresponded to that which occurred over the first few lake transect stations (R11–R14), all of which were within only 0.4 m of Gollum's Lake.

DISCUSSION

THE EFFECT OF SULFIDE

The environmental factors potentially responsible for community boundaries in the soft-bottom benthos around the brine seep were evaluated by Powell *et al.* (1983). These included oxygen content, salinity, and sulfide concentration. Powell *et al.* (1983) concluded that soft-bottom community boundaries were determined primarily by the sulfide content of the overlying water.

Powell *et al.* (1983) never found oxygen concentrations below approximately 3 ppm outside of Gollum's Lake. Changes in O_2 normally affect community structure only when levels drop below 1 ppm (Rhoads and Morse 1971, Rosenberg 1977, Jørgensen 1980). Consequently, oxygen cannot be a limiting factor beyond the boundaries of Gollum's Lake and probably does not affect any of the community boundaries on the hard bottom surrounding the EFG brine seep.

Salinity is known to affect community structure in the vicinity of anthropogenic brine discharges (Mackin 1973, Moseley and Copeland 1974), but it is unlikely that salinity is the principal cause of community differences at the EFG brine seep except in Gollum's Lake and the upper part of Gollum's Canyon above Corner Pool (see Figure 1) where salinities are above 50‰ (Powell *et al.* 1983). Although the community distinctions on Cottonwick Rock are quite clear, the change in salinity along this vertical transect was less than 3‰ (Figure 2). The greatest change in community composition occurred between station R1 on the canyon floor and replicates R2 and R3 0.3 m above the canyon floor, yet salinity changed by only 1‰ between these stations. In addition, salinity at R11 nearest Gollum's Lake was essentially equivalent to normal seawater salinity at these depths, even though R11 was taxonomically unique among the lake transect stations but very similar to R2–R5 of the Cottonwick Rock transect. Therefore, salinity differences cannot adequately explain variations in community characteristics and salinity does not appear to be an important factor in delimiting community boundaries on the hard bottom any more than it was on the soft bottom studied by Powell *et al.* (1983).

Although sulfide rarely is considered among the factors determining taxonomic composition in benthic habitats, enough information is available to suggest that it may be an important factor affecting many benthic macrofauna (Groenendaal 1979, Felbeck *et al.* 1981, Childress and Mickel 1982, Shumway and Scott 1983) as well as the more widely known effects on meiofauna community structure (Crezee 1976, Farris 1976, Powell and Bright 1981, and others). Sulfide is a potent metabolic toxin which is lethal to most invertebrates at concentrations of less than 1 ppm (Powell *et al.* 1979). This concentration is comparable to that found near the canyon floor at R1 on the Cottonwick Rock transect. Sulfide concentration was approximately 45 μg atoms$\cdot 1^{-1}$ (about 1.4 ppm) at R1, but fell to $\sim$ 5 μg atoms$\cdot 1^{-1}$ at about 1 m above the bottom (near stations R4 and R5). Sulfide concentration at R11

nearest Gollum's Lake was ~ 5 μg atoms·1^{-1} and ~ 1 μg atoms·1^{-1} at R12 and R13 located on the lake's sandy shoreline (Powell *et al.* 1983). Although unmeasured, sulfide concentration was probably below detection limits at the remaining lake transect stations (R14–R18). The changes in taxonomic composition between Cottonwick Rock station R1 and replicates R2 and R3 coincide with a 50% reduction in sulfide concentration. The faunal change from R2 and R3 to R6 and R7 on the Cottonwick Rock transect, and from R11 to R13 and R14 on the lake transect coincides with an additional ~100% drop in sulfide concentration. Although the turbulent flow of the brine stream, as evidenced by the vertical heterogeneity in sulfide concentration in Figure 2, guarantees considerable temporal variability in the sulfide concentration impacting Cottonwick Rock stations, the drop in sulfide concentration is dramatic and occurs over a sulfide concentration range known to be within the toxicity range for many organisms (Lasserre and Renaud-Mornant 1973; Oseid and Smith 1974a, b). Thus, sulfide appears to be an important environmental factor controlling taxonomic composition along both transects. The similarity between the taxonomic changes over the entire Cottonwick Rock transect (~2m) and between R11 and R14 (~0.6m) on the lake transect might be attributed to the more gradual, vertically extensive sulfide gradient present in the canyon brine stream which affects the entire Cottonwick Rock transect and to the much sharper gradient of Gollum's Lake which affects only those stations very near the lake.

Further supporting this conclusion is the fact that similar changes in community structure occurred in the soft-bottom benthos on a transect including Gollum's Canyon and stations downstream of the canyon mouth where sulfide was found to be the principle factor determining soft-bottom macro- and meiofaunal community boundaries (Powell *et al.* 1983). In particular, soft-bottom stations near Cottonwick Rock, which were classified as thiobiotic by Powell and Bright (1981) and Powell *et al.* (1983), had high abundances of amphipods, nereid polychaetes and oligochaetes, as did station R1 on the canyon floor. Oxybiotic stations located on the soft-bottom downstream of the canyon mouth had higher abundances of tanaidaceans and isopods and fewer amphipods, as did R2 and R3. In addition, soft-bottom control stations were similar to R17 and R18, in that few tanaidaceans and amphipods were found relative to other stations, annelids constituted an important control station macrofaunal group with syllids dominant, and total abundances were considerably below most other stations. Curiously, as was found at soft-bottom stations by Powell *et al.* (1983), amphipods, along with some annelids, appeared to be the macrofaunal group most tolerant to sulfide in spite of the fact that, as a group, amphipods are thought to have a low tolerance to either low oxygen or high sulfide concentration (Wieser and Kanwisher, 1959; Theede 1973; Oseid and Smith 1974a, b).

Rhoads and Morse (1971) found that few calcareous organisms were present in communities where 0_2 levels were below 1 ppm. In this study, molluscs, in general, were found in highest abundance at stations with the lowest sulfide concentrations even though 0_2 concentration was not limiting

at any of the stations sampled and even though some molluscs prefer sulfide-rich habitats (Felbeck 1983; Felbeck, Childress, and Somero 1981). The data suggest that the observations of Rhoads and Morse (1971) may be explained partially on the basis of sulfide tolerances as well as low O_2 tolerances, because benthic areas examined by them are also likely to be areas of high interstitial sulfide concentration.

THE EFFECT OF FOOD SUPPLY

The changes in taxonomic composition and faunal abundance cannot be ascribed simply to the effect of a sulfide gradient, however. Food supply also may be important. A "halo" effect has been observed for both anthropogenic and natural discharge systems (Mackin 1973, Davis and Spies 1980, Straughan 1982) whereby microflora and microfauna dominate and are in high abundance near the discharge but macrofauna are poorly represented. Benthic meio- and macrofauna peak in abundance at different distances from the discharge, depending on the tolerance of the organisms to the stresses imposed by the discharge. In these areas, due to an increase in food produced by the large microfloral populations often present, absolute abundances can be considerably above control levels even for those taxa also present in nearby, unstressed areas. In general, changes in taxonomic composition tend to occur at higher taxonomic levels (*e.g.* family or phyla *vs.* species and genera) with increasing stress (Boesch and Rosenberg 1981), and taxonomic composition tends to return to that of control areas before numerical abundance (Pearson 1981).

Besides the taxonomic changes previously discussed, stations near the brine seep had marked increases in abundance of most taxa. Along the Cottonwick Rock transect, peak overall abundances were seen just above the canyon floor, and the totals for all stations on this transect were significantly higher than lake transect totals ($p < .05$, Mann-Whitney Test). Even the uppermost stations, R6 and R7, had abundances nearly five times higher than control stations. Total abundances were also substantially above control levels at the lower lake transect stations, R11–R14.

Bright *et al.* (1980a, b) suggested that the increase in faunal abundance was due to the advection of sulfur bacteria from the brine lake and canyon into the peripheral communities. Certainly, both the lake interface and canyon floor harbor greatly increased populations of sulfur bacteria. Visual observations by Bright *et al.* (1980a, b) and Powell *et al.* (1983) indicated that portions of the benthic bacterial mat and the bacterial population at the lake-seawater interface are advected downstream by the brine flow more or less continually. ATP concentrations above the lake and in the canyon were higher than those normally found in water of this depth at the EFGB (Bright *et al.* 1980a), and are suggestive of a similar increase in bacterial biomass often found associated with chemoclines (Karl, LaRock, and Shultz 1977; LaRock, Lauer, Schwarz, Watanabe, and Wiesenburg 1979). Furthermore, the polychaete fauna near the seep included an important filter-feeding

component not prominent elsewhere, which suggests an increase in the food supply in suspension.

As sulfide is diluted by turbulent mixing, the amount of food available from the brine seep system also is diluted, but, because sulfide reacts spontaneously with oxygen, the area affected by an increased food supply should be greater than that affected by the presence of sulfide. Near Gollum's Lake, the effect of the brine is localized because movement of materials across the lake-seawater interface is inhibited by a sharp density gradient. Nevertheless, the brine lake apparently influences the peripheral hard bottom up to about 1 m above the shoreline. In the canyon, because of turbulent mixing, the brine stream influences the fauna at least 2 m above the canyon floor (the uppermost stations sampled). In both cases, these effects apparently extend beyond the influence of sulfide. For example, both stations R6 and R7 at the upper end of the Cottonwick Rock transect and all lake transect stations, except perhaps R11, had sulfide concentrations well below $\sim 5\ \mu g\ atoms \cdot l^{-1}$. Powell *et al.* (1983) found that thiobios were dominant only where sulfide was considerably above this value. In fact, using this criterion, the only thiobiotic station sampled in Gollum's Canyon was R1.

Nevertheless, the data suggest that some taxa are more sulfide tolerant than others and that this fact plus an increase in food supply near the brine source (the lake edge or canyon floor) results in the changes in faunal composition observed. If both the sulfide and food gradient are important, but one (food) extends beyond the other, one might expect the abundance of sulfide-tolerant taxa, most of which are poorly represented at control stations, to increase with an increase in food supply near the brine source (the lake edge or canyon floor) even where sulfide is present. In contrast, the abundance of those taxa dominant at control stations should increase as food supply increases only at stations outside the area where sulfide is a limiting factor. Nearer the brine source, their numbers should decrease. Thus, for sulfide-tolerant taxa, absolute abundances (number collected per unit area) and relative abundances (percentage of total organisms collected) should both increase along a transect from the control stations to the brine source and be correlated significantly. On the other hand, the relative abundances of taxa typical of control stations should decrease throughout the transect as the numbers of sulfide-tolerant taxa increase. Their absolute abundances, however, should increase initially because more food is available and then decrease as sulfide becomes a limiting factor; thus their relative and absolute abundances should be correlated poorly.

In fact, high absolute and relative abundances of some taxa (*e.g.* tanaidaceans, amphipods and nereids) occurred simultaneously at the lake or canyon floor end of the transects (R1, R2, R3, R11) and were significantly correlated (Table 4). Both relative and absolute abundances of these sulfide-tolerant taxa tended to decrease significantly with distance from the brine source. Crustaceans, for example, were relatively and absolutely more abundant at stations R1–R5 and R11 than elsewhere. Certainly, such taxa

TABLE 4

Correlation coefficients for regressions of absolute numbers (Tables 1, 2) versus relative abundance for the individual taxa: * indicates a significant regression with a slope significantly different from 0 ($\alpha \pm 0.05$); + indicates taxa where no more than 1 of the top 3 stations ranked by absolute abundance was also among the top 3 when ranked by relative abundance.

Taxon	r
Scyphozoa	.38
Annelida	.29 +
Mollusca	.73 +
Sipuncula	.57*+
Tanaidacea	.89*
Amphipoda	.98*
Isopoda	.88*
Capitellidae	.52
Chrysopetalidae	.55*+
Cirratulidae	.90*
Dorvilleidae	.95*
Eunicidae	.95*
Maldanidae	.89*+
Nereidae	.99*
Sabellidae	.97*
Spionidae	.71*
Syllidae	.51

owe their dominance at these stations to the presence of sulfide and the additional food source generated by it.

In contrast, for most of the taxa characteristic of control stations and those present in relatively high abundance at those intermediate lake transect stations which clustered with R17 and R18 (*e.g.* sipunculans, scyphozoans, molluscs and annelids—especially syllids and chrysopetalids), high absolute abundances are poorly correlated with high relative abundances. Either the regression between the two was not significant or at least two of the top three stations as ranked by absolute abundance were not among the top three if ranked by relative abundance for these taxa (Table 4). In this case, to the extent that sulfide remains below toxic levels, an increased food supply may increase the abundance of these taxa at stations nearer the lake or canyon floor end of the transects. Sipunculans, for example, were most abundant near Gollum's Lake (R11–R13) but relative abundances were highest at control stations. Molluscs outnumbered crustaceans only at control station R18, although total abundances of both groups were con-

siderably below peak abundances found at other stations. Thus, the community structure resembles the "halo" model found for other discharge systems for which an increased food supply has been postulated as an important determinant affecting biotic composition (Spies and Davis 1979, Davis and Spies 1980) and suggests that both the presence of sulfide and an increase in food supply are important factors affecting the hard-bottom fauna near the EFG brine seep.

The community structure of most nearshore and estuarine benthic communities is thought to be affected by physical disturbance (Gray 1977, Woodin 1978, Thistle 1981), predation (Virnstein 1977, 1979; Thistle 1982), and competition for space (Peterson 1977, Peterson and Andre 1980, Schoener 1982). Although the importance of competition for food has been discussed (Levinton 1972, Underwood 1978, Bianchi and Levinton 1981), food-limitation as a community-wide phenomenon on the hard bottom is only obvious in the deep sea (Lonsdale 1977, Ballard and Grassle 1979). The extent to which these factors affect continental shelf communities in the Gulf of Mexico is, however, poorly understood (Flint and Rabalais 1981, Flint and Holland 1980).

The EFG brine seep is similar to the deep-sea hydrothermal vent communities in that a sulfide-based primary food source is advected to the peripheral benthic community (Bright *et al.* 1980b). The data suggest that the fauna of the EFG deep reef normally are food-limited, and are so in spite of the general abundance of macro-algae and the potentially highly productive, shallow-water reef just upslope of these habitats. Abundances increased by 5 to 10 times near the brine lake and canyon floor. This increase included both taxa characteristic of control stations, which probably utilize the same microhabitats at stations closer to the brine source, and taxa characteristically found in high abundances only at stations near the brine source (R1–R3, R11), many of which must occupy similar, if not identical, microhabitats. Although differential rates of predation could be utilized as an alternative hypothesis (Glynn 1976), it is difficult to see why predators should be less active near the seep, particularly when visual observations of feeding fish indicate that feeding in the canyon and above the lake commonly occurs (Bright *et al.* 1980b). Although competition for space is an important determinant of community structure for the encrusting fauna of shallow-water reefs (Lang 1973, Porter 1974), and other hard-bottom communities, it is unlikely to be of comparable importance in a situation where total macrofaunal abundance can be increased 5 to 10 times over control levels without fundamental changes in taxonomic composition (*e.g.* compare R6, R7 with R17, R18). The increased abundances near the seep, therefore, suggest that certain faunal elements of the outer continental shelf deep-water reefs, like the EFG, are food limited. This limitation appears to be a general one rather than being restricted to a particular predator-prey interaction (Underwood 1978) or trophic level (Dayton and Hessler 1972). To this extent, the hard-bottom community adjacent to the EFG brine seep differs from most other nearshore hard-bottom com-

munities studied previously but resembles those found near the hydrothermal vents in the deep sea.

The data also suggest that, as in the case of deep-sea vent communities, sulfur bacteria can serve as an important primary food source for macrofaunal food webs, although the importance of meiofauna as an intermediate step remains an interesting possibility (Kuipers, de Wilde, and Creutzberg 1981; Gerlach 1978). Although the significance of sulfur bacteria as a food source in most benthic food webs remains poorly understood, their importance is likely dependent on their relative abundance and accessibility rather than the ability of macrofauna to utilize them directly or indirectly as a food resource.

ACKNOWLEDGMENTS

Dr. R. Farris and S. Jameson provided invaluable help on the cruise. Our special thanks to them, the scientists and staff of the Harbor Branch Foundation, and the crew of the R/V JOHNSON and research submersible JOHNSON SEA-LINK whose extra effort before and during the cruise made it a success. J. Kendall, S. Connor, and A. Woods helped with mobilization for the cruise. Drs. R. Rezak, J. Wormuth, D. Boesch, Mr. J. Parrack, and two anonymous reviewers offered suggestions that improved the manuscript. We thank M. Harrison and J. Frederick who typed the manuscript and prepared some of the tables.

This material is based upon work supported by grants and contracts from NOAA Office of Coastal Zone Management No. NA80AA-H-CZ118, the National Science Foundation No. OCE-8019458 and the USDOI Minerals Management Service No. AA851-CTO-25 to E. Powell and T. Bright. Any opinions, findings and conclusions or recommendations expressed in this publication are those of the authors and do not necessarily reflect the views of NOAA-OCZM, NSF or MMS.

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Contributions in Marine Science. (1984) Vol. 27:127–141.

COMPONENTS OF THE SESTON AND POSSIBLE AVAILABLE FOOD FOR OYSTERS IN GALVESTON BAY, TEXAS[1]

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ABSTRACT

Seasonal changes in components of the seston such as particulate lipid, carbohydrate and protein as well as chlorophyll *a*, particulate inorganic matter (PIM), ash-free dry weight (AFDW) and seston dry weight (DW) were measured over an annual cycle in Galveston Bay, Texas. Food for the oyster was defined as the sum of the concentrations of lipid, carbohydrate and protein; a food index was calculated as the percentage food in the total seston.

Wind speed appears to be an important forcing function, especially in regard to its ability to resuspend bottom material. PIM and non-algal material dominate the suspended particulate matter available as potential food for oysters. Chlorophyll *a* concentrations, the "food" measure, and the food index were intercorrelated and were higher in the spring and summer than in the fall and winter. Presumably, the nutritional quality of the seston was greater during the spring and summer period.

Accepted 27 February 1984

INTRODUCTION

Suspended particulate matter or seston in the water column originates either from fresh inputs into the system or from resuspended bottom sediments. The seston includes living plankton, organic detritus and inorganic particles. Changes in the composition of the seston imply changes in the nutritional quality of the food available to filter feeding organisms.

As Widdows, Fieth, and Worrall (1979) point out, our present understanding of the effects of food concentration on the feeding of bivalves is derived

mainly from laboratory experiments using unicellular algal suspensions as the food source. These studies are not directly applicable to natural estuarine conditions where silt often forms the major component of the total seston. In fact, growth rates of the mussel *Mytilus edulis* fed pure algal suspensions have not equalled the maximum growth rates observed in nature. Kiørboe, Møhlenberg, and Nøhr (1981) were able to obtain a growth rate comparable to maximum growth rates only when 5 mg/l of silt was added to a pure algal suspension.

A number of studies have been conducted on components of the seston presumably available as food for oysters and other estuarine filter feeders. Diatoms (Dean 1887, Lotsy 1896, Moore 1907), nannoplankton (Lipschütz 1913, Martin 1923, Nelson 1925), organic detritus (Petersen 1908, Petersen and Jensen 1911, Blegvad 1914), bacteria (Zobell and Feltham 1938), and small animal forms (Nelson 1921) have all been proposed as sources of food for filter feeders.

One approach to measuring food for filter feeders is to evaluate the nutritional quality of particles within an appropriate size range. It was the purpose of this study to quantify components of the seston and to evaluate natural seasonal changes in the food available to the oyster, *Crassostrea virginica*. The relationship between changes in potential food and oyster composition and condition will be discussed in a subsequent paper.

METHODS

The overall plan of the study was to measure environmental parameters and components of the seston over an annual cycle. Samples were taken twice a month from 5 September 1980 to 3 September 1981 from a pier over April Fool reef (Fig. 1).

Temperature was measured with a mercury thermometer to the nearest 0.1°C. Salinity was determined (±0.5 ‰) using an American Optical Refractometer. Water transparency was measured by recording the depth at which a Secchi disk just disappeared from view (herein defined as the Secchi depth). The time necessary for a drogue to traverse a known distance was used to calculate current speed. Current direction was determined by measuring the direction of flow of the drogue with an engineer's compass; direction was measured in compass degrees to the right of 0°N. Wind speed and direction data were obtained from the National Weather Service in Galveston, Texas.

Seston samples were obtained by use of a pumping/filtering system which was used to pump water from about 0.3 m above the bottom. The components of the pumping/filtering system are shown in Figure 2. The 115-volt pump was powered by a 400-watt Honda generator. Water was pre-filtered through a cartridge unit containing a 300-μm mesh filter (Fig. 2, U). A valve (Fig. 2, V) was inserted between the cartridge unit and a 293-mm filter unit (Fig. 2, M). the amount of water filtered was measured into a calibrated carboy (Fig. 2, C). Hoses and connectors were of the standard garden variety. A high pressure hose (rated to 250 psi), however, was used on the intake side of the pump to prevent hose constriction. The intake hose was held down by a weight about 0.3 m from its end and held off the bottom by an attached float. The valve on the pumping/filtering unit was used to control the flow rate and to obtain 250 ml of water for analysis of seston dry weight (DW), ash-free dry weight (AFDW), particulate inorganic matter (PIM) and chlorophyll *a*. The material retained on the 293-mm diameter filter was used for the determination of lipids, carbohydrates and proteins.

Filters used in the determination of DW and AFDW (American Public Health Association 1971) were rinsed with distilled water. Chlorophyll *a* concentrations were measured by the

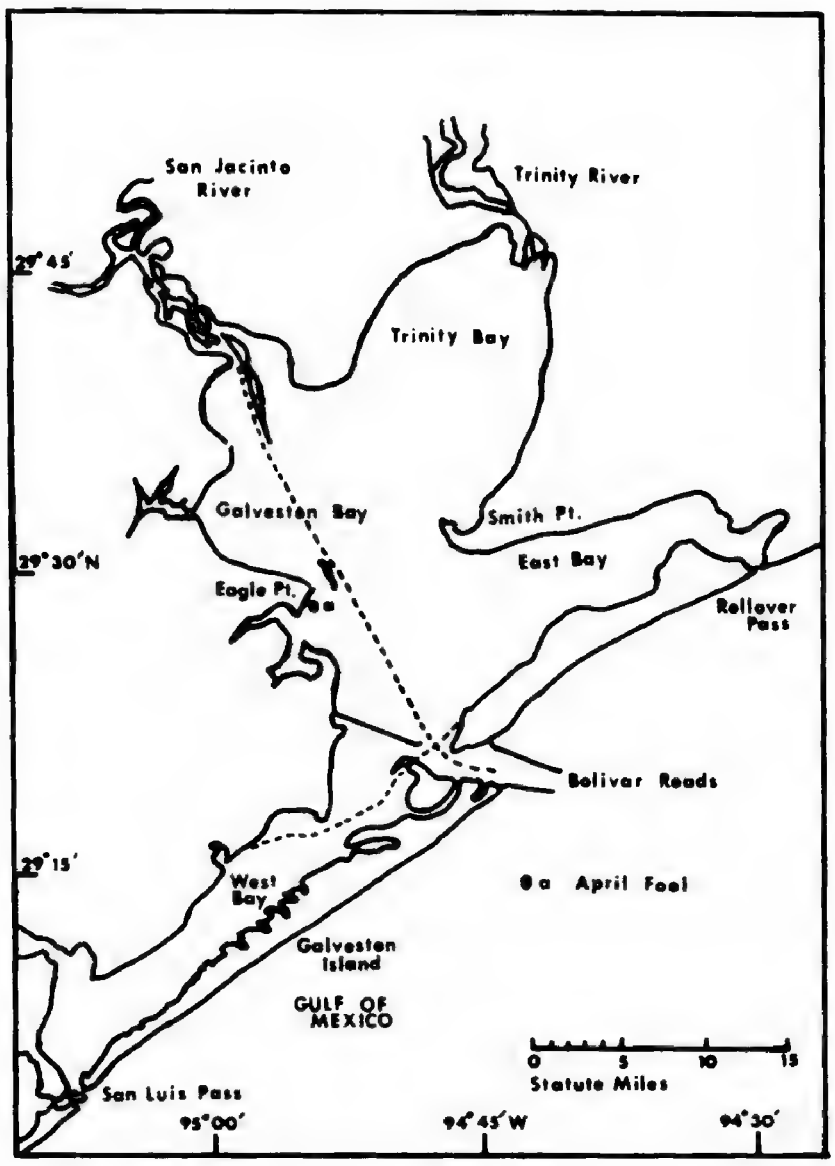

FIG. 1. Map of the Galveston Bay area showing the sampling station.

fluoromatic method of Strickland and Parsons (1968) and converted to carbon equivalents using a carbon to chlorophyll *a* ratio of 26 (based upon *Skeletonema costatum*; Parsons, Stephens, and Strickland 1961). Carbon was converted to organic matter equivalents (organic matter = carbon × 2.14) in a manner identical to that of Widdows *et al.* (1979). All measures were made in triplicate and every filter used was a Gelman type A/E glass fiber filter (0.45 μm effective pore size).

From 12.1 to 59.0 liters of water were filtered onto the 293-mm diameter filters. Lipids, carbohydrates and proteins in the seston were extracted and analyzed by a process modified from Holland and Gabbot (1971). The samples and a filter blank were freeze-dried and homogenized for 1 min in 100 ml of 2:1 chloroform:methanol. The homogenate was then filtered through a 47-mm diameter filter, and the lipid-containing filtrate was evaporate at 40–50°C overnight. The lipids were redissolved in 10 ml of chloroform and passed through a 25-mm diameter filter into a small vial into which 2 ml of double distilled water was later injected. These latter steps were necessary to remove the salt which was observed in the initial chloroform:methanol extract. Three 1 ml aliquots of the chloroform solution were pipetted onto pre-weighed 47-mm filters, dried for 5 min at 40–50°, desiccated for 20 min and then weighed.

Carbohydrates in the residue were dissolved in 100 ml cold, 5% trichloroacetic acid. After allowing the sample to stand for 10 min at 4°C, the solution was passed through a 47-mm filter. The carbohydrate concentration was determined (Strickland and Parsons 1968) with anhydrous dextrose as a standard.

One hundred ml of 1N sodium hydroxide was added to the remaining residue. The sample was heated for 30 min at 56°C. The protein concentration was then determined by the method of Lowry, Rosenbrough, Farr, and Randall (1951) using bovine serum albumen as a standard.

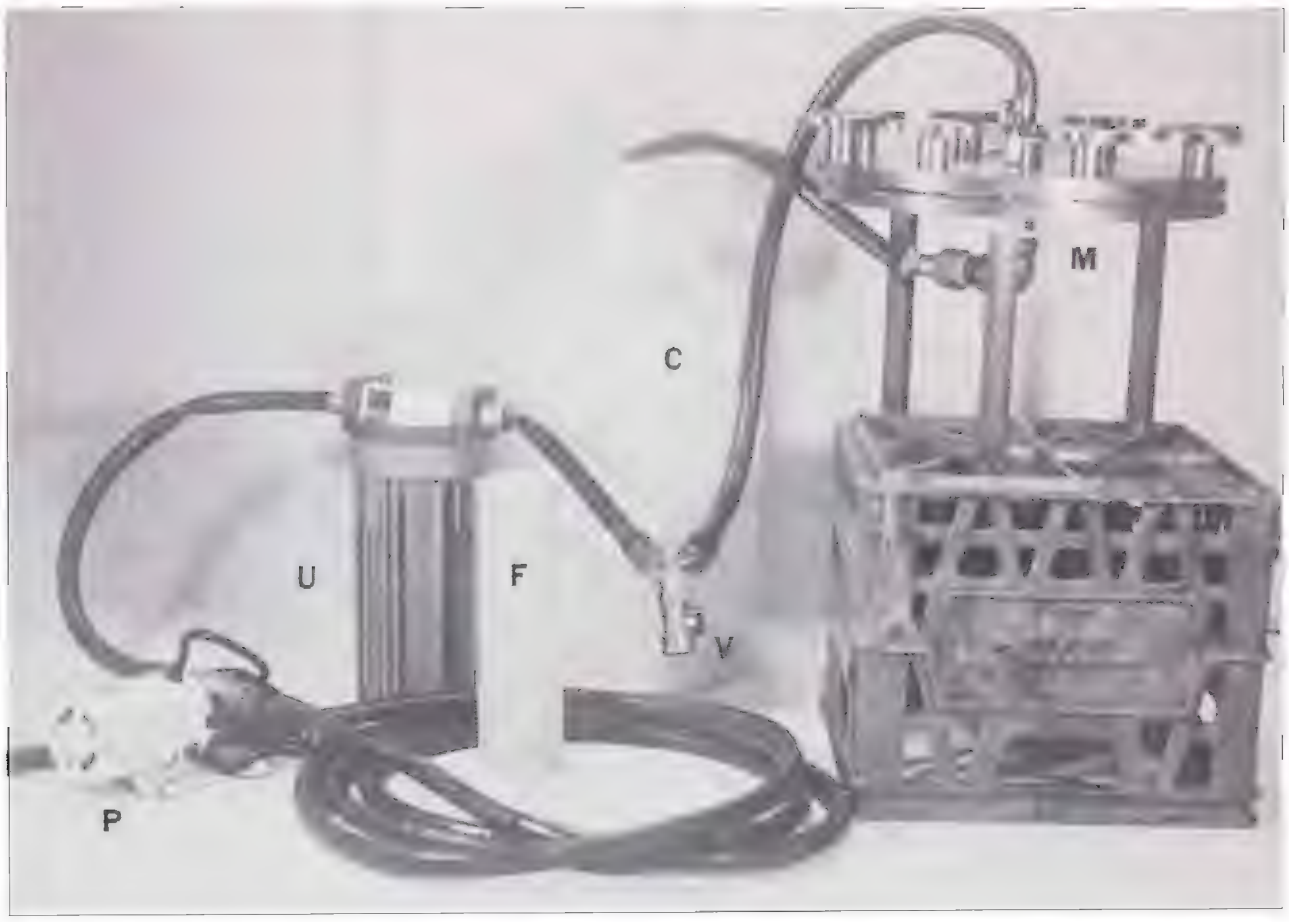

FIG. 2. Photograph of the pumping/filtering system showing the various components. P, pump; U, cartridge unit; F, cartridge filter; V, valve; M, primary filter (Millepore); C, carboy.

A "food" measure was defined as the sum of the concentrations of lipid, carbohydrate and protein. A food index was calculated as the percentage food in the seston—that is, food index = "food"/DW × 100 (Widdows *et al.* 1979).

Two special samplings were made to determine the precision of the extraction/analytical scheme. Water was pumped up and prefiltered in the usual manner. The pre-filtered water was directed through a "T" connection which simultaneously routed the water into two 20-l carboys. The contents of the carboys were then filtered through the 293-mm filter unit. The values from these nearly simultaneous samples were used as a measure of the error of the extraction/analytical procedure.

The Kruskal-Wallis one-way analysis of variance (Hull and Nie 1981), a non-parametric test, was used to test the null hypothesis of no differences in the mean values of the seston measurements from one sampling day to another (see Daniel 1978). Measurements from daily samples were grouped by season and a seasonal mean was calculated. Day-to-day and season-to-season differences were identified by the multiple comparison technique of Dunn (1964). An experiment error rate of $\alpha = 0.25$ was used for day-to-day comparisons, whereas $\alpha = 0.15$ was employed in the season-to-season comparisons. Spearman's rank-order correlation coefficients (r_s) were calculated to ascertain the degree of association among the various components of the seston and between seston measurements and physical parameters (Hull and Nie 1981). Further details about the sampling site and methods are provided by Soniat (1982).

RESULTS

Values of the physical parameters for each sampling date are shown in Table 1. Salinity over the sampling period ranged from 5 to 28.5‰. Temperature peaked at 30.0°C during July and early August of 1981; a minimum temperature of 9.3°C was recorded during February, 1981. Water

TABLE 1

Values of environmental parameters for a sampling day. Wind data are from the National Weather Service, Galveston, Texas.

Date	Salinity (ppt)	Temperature (°C)	Average Wind Speed (mph)	Wind Direction	Secchi Depth (m)	Current Direction (degrees)	Current Speed (cm/sec)
09/05/80	22.5	28.0	17.0	NE	0.28	225.0	17.4
09/19/80	20.5	29.0	9.6	E	0.53	206.0	8.4
10/03/80	18.0	25.0	8.9	NE	0.46	194.0	7.6
10/17/80	21.0	24.0	12.5	S	0.30	5.0	11.7
11/07/80	20.0	19.0	11.2	S	0.61	27.5	11.2
11/21/80	21.0	12.0	8.5	NE	0.76	199.0	10.2
12/05/80	23.5	15.0	10.9	SE	0.76	230.0	5.9
12/18/80	23.0	16.0	11.7	S	0.66	9.0	14.6
01/03/81	23.0	14.0	6.5	SE	0.91	277.5	1.8
01/16/81	22.5	11.0	12.6	NE	0.36	200.0	10.5
02/06/81	23.0	9.3	11.0	NE	0.79	193.0	14.2
02/19/81	22.5	13.1	9.3	SW	0.19	205.0	7.2
03/05/81	23.5	18.0	13.3	N	0.58	167.5	11.2
03/20/81	23.5	15.1	9.3	SE	0.19	202.0	5.6
04/03/81	28.5	21.0	15.4	S	0.28	40.5	3.7
04/15/81	27.5	24.0	9.9	SE	0.66	253.0	5.3
05/05/81	18.0	25.0	8.0	S	0.66	350.5	4.4
05/21/81	17.5	23.0	14.5	SE	0.20	347.0	9.2
06/04/81	21.5	27.0	15.7	SE	0.30	349.5	13.7
06/18/81	5.0	29.0	4.7	S	0.53	358.5	5.7
07/02/81	5.5	30.0	10.1	SW	0.66	51.0	4.8
07/16/81	7.0	30.0	9.5	S	0.76	75.0	2.8
08/07/81	14.0	30.0	9.0	W	0.66	96.0	6.6
08/20/81	15.5	29.0	9.2	NE	0.30	192.0	10.2
09/03/81	14.0	28.0	8.8	S	0.64	177.5	4.1

transparency varied greatly, even between adjacent sampling periods, and the secchi depth ranged from 0.19 to 0.91 m. Current speeds during fall and winter were generally greater than those of spring and summer. Relationships among some physical parameters and selected components of the seston are presented in Table 2. As indicated by the Spearman rank correlation coefficient (r_s), wind speed and current speed are significantly correlated. Seston DW, AFDW and PIM form a closely correlated group of measures and are all inversely correlated with water transparency. Wind speed, but not current speed, was significantly correlated with water transparency.

The results of the two special samplings (conducted to determine the precision of the extraction/analysis procedure for lipid, carbohydrate and protein) are shown in Table 3 and indicate a fairly good correspondence between the samples. These results are an estimation of analytical precision; the variability of the technique is relatively small when compared to the variation within and between sampling days.

Kruskal-Wallis tests on the various measures of the seston were all significant ($p < 0.001$) and indicate that there were real differences between sampling days. These day-to-day as well as season-to-season differences, are easily gleaned from Tables 4 and 5. Mean values for the seston

TABLE 2

Spearman rank-order correlation coefficients and level of significance for selected physical parameters and seston dry weight (DW), particulate inorganic matter (PIM) and ash-free dry weight (AFDW). $N=25$.

	Wind speed	Secchi depth	DW	PIM	AFDW	Current speed
Wind speed	-	-0.39*	0.73***	0.72***	0.61***	0.56**
Secchi depth	-	-	-0.52**	-0.50**	-0.53**	-0.24
DW	-	-	-	0.99***	0.93***	0.49**
PIM	-	-	-	-	0.91***	0.46**
AFDW	-	-	-	-	-	0.45*

*$p < 0.05$ **$p < 0.01$ ***$p < 0.001$

parameters are plotted in Figures 3 to 6. The concentrations of protein, lipid and carbohydrate tended to vary together; however, from mid-March to mid-August protein concentrations were at elevated levels (Fig. 3). The average protein concentration over the sampling period was 0.80 mg/l and daily means ranged from 0.13 to 1.73 mg/l. Peaks in the lipid concentrations correspond closely to the carbohydrate peaks throughout the year. The average concentration was 0.34 mg/l with a range of 0.14 to 0.85 mg/l in the daily means. The carbohydrate component was always much lower in

TABLE 3

Results showing the precision of the extraction and analysis of lipid, carbohydrate and protein in the seston.

	Sample 1 (µg/ℓ)	Sample 2 (µg/ℓ)	Coefficient of Variation
01/29/81			
Lipid	420.00	465.00	7.19
Carbohydrate	15.55	13.19	11.61
Protein	144.15	146.40	1.10
03/20/81			
Lipid	555.98	514.85	5.43
Carbohydrate	202.28	208.17	2.03
Protein	1224.98	1239.70	0.84

concentration than were the lipid and protein constituents of the seston. Daily mean values ranged from 1.9 to 397.7 µg/l with an overall mean of 66.2 µg/l.

Seston DW and PIM varied greatly over the year and varied closely together (Fig. 4, Table 2). The area between the curves in Figure 4 (the difference between DW and PIM weight) is a measure of the AFDW in the seston. The average DW and PIM weight was 54.4 and 46.1 mg/l, respec-

TABLE 4

Mean daily and seasonal ranks for protein, lipid, carbohydrate and the food index from the Kursal-Wallis analysis of variance. Daily means are based upon $N=3$ determinations. Daily means are grouped by season for the calculation of seasonal ranks. Fall means are based upon 7 daily means; other seasonal means are based upon 6 daily means. Differences between daily mean ranks > 54.63 are statistically significant ($\alpha = 0.25$). Differences between the fall and other seasonal ranks > 9.13, and differences between the other seasonal ranks > 9.28, are significant ($\alpha = 0.15$).

	Protein		Lipid		Carbohydrate		Food Index	
Date	Mean Ranks	Seasonal Ranks	Mean Ranks	Seasonal Ranks	Mean Ranks	Seasonal Ranks	Mean Ranks	Seasonal Ranks
09/05/80	42.67		74.00		68.00		21.00	
09/19/80	24.33		14.00		59.33		16.67	
10/03/80	30.67		54.33		61.67		20.83	
10/17/80	17.00	24.62 (Fall)	53.00	37.38 (Fall)	41.67	38.62 (Fall)	2.33	22.17 (Fall)
11/07/80	13.33		24.00		20.33		5.33	
11/21/80	3.33		29.33		4.00		34.67	
12/05/80	28.00		55.33		71.33		37.50	
12/18/80	5.33		13.00		16.00		9.67	
01/03/81	6.33	24.06 (Winter)	43.00	39.33(Winter)	50.67	51.89(Winter)	36.83	35.86 (Winter)
01/16/81	24.67		54.33		57.00		13.50	
02/06/81	32.67		8.33		50.67		48.33	
02/19/81	47.33		62.00		65.67		69.33	
03/05/81	13.33		37.67		25.33		29.50	
03/20/81	57.67		67.33		69.33		66.33	
04/03/81	65.33		56.33		13.33		24.00	
04/15/81	45.00	52.94 (Spring)	21.00	48.28(Spring)	27.00	32.44(Spring)	51.00	45.11 (Spring)
05/07/81	68.00		41.67		9.00		66.00	
05/21/81	68.33		65.67		50.67		33.83	
06/04/81	60.67		18.33		24.67		19.50	
06/18/81	57.67		31.33		33.67		74.00	
07/02/81	51.67	52.61(Summer)	15.00	27.11(Summer)	31.67	28.95 (Summer)	59.67	51.50 (Summer)
07/16/81	44.67		24.33		36.67		63.67	
08/07/81	30.67		16.67		3.33		50.67	
08/20/81	70.33		57.00		43.67		41.50	
09/03/81	41.00		13.00		15.33		54.33	

tively. At all times, the amount of inorganic matter exceeded the AFDW. The AFDW was usually a very small proportion of the total dry weight of the particulate matter. The "food" measure (the sum of lipid, carbohydrate and protein concentrations) averaged 1.3 mg/l, whereas AFDW averaged 8.7 mg/l, which is an almost sevenfold difference.

The food index varied markedly throughout the year. Mean food index values on a sample day ranged from 0.6 to 11.0% with an overall mean of 3.6%. The food index was generally higher in the spring and summer than in fall and winter (Fig. 5, Table 4). Over fall and winter, only one high food index value was recorded (in late February).

TABLE 5

Mean daily and seasonal ranks for chlorophyll *a* (CHL), dry weight (DW), particulate inorganic matter (PIM) and ash-free dry weight (AFDW) from the Kursal-Wallis analysis of variance. Daily means are based upon $N=3$ determinations. Daily means are grouped by season for the calculation of seasonal ranks. Fall means are based upon 7 daily means; the other seasonal means are based upon 6 daily means. Differences between daily mean ranks > 54.63 are statistically significant ($\alpha = 0.25$). Differences between the fall and other seasonal ranks > 9.13, and differences between the other seasonal ranks > 9.28, are significant ($\alpha = 0.15$).

	CHL		DW		PIM		AFDW	
Date	Mean Ranks	Seasonal Ranks	Mean Ranks	Seasonal Ranks	Mean Ranks	Seasonal Ranks	Mean Ranks	Seasonal Ranks
09/05/80	64.33		69.33		69.00		73.00	
09/19/80	42.67		46.67		46.67		54.67	
10/03/80	46.33		51.00		50.33		58.00	
10/17/80	18.67	35.05 (Fall)	69.00	45.50 (Fall)	69.67	45.19 (Fall)	69.67	39.76 (Fall)
11/07/80	10.00		52.00		52.67		49.67	
11/21/80	18.00		9.00		7.67		14.00	
12/05/80	53.67		43.67		43.33		52.00	
12/18/80	6.33		41.33		41.00		35.50	
01/03/81	6.67	30.00(Winter)	19.67	32.34(Winter)	18.67	31.78(Winter)	18.67	31.25 (Winter)
01/16/81	40.67		57.00		58.33		39.67	
02/06/81	12.33		24.67		23.00		26.33	
02/19/81	60.33		7.67		6.33		15.33	
03/05/81	19.00		37.33		39.00		25.00	
03/20/81	41.67		26.17		24.00		32.00	
04/03/81	17.00		71.33		72.33		63.17	
04/15/81	20.67	37.67 (Spring)	35.33	44.30 (Spring)	33.00	44.00 (Spring)	41.17	42.89 (Spring)
05/07/81	62.33		32.33		32.00		32.33	
05/21/81	55.33		63.33		63.67		63.67	
06/04/81	30.00		67.00		65.33		63.17	
06/18/81	68.33		2.00		2.00		18.67	
07/02/81	65.00	49.78(Summer)	16.33	28.61(Summer)	15.50	29.83(Summer)	15.33	26.81 (Summer)
07/16/81	32.33		7.33		11.17		3.50	
08/07/81	29.33		21.00		28.33		3.50	
08/20/81	73.67		58.00		56.67		56.67	
09/03/81	45.33		21.50		20.33		25.33	

Chlorophyll *a* tended to be higher in concentration in spring and summer than at other times of the year (Fig. 6, Table 5). Peaks in concentrations of the pigment, however, occurred throughout the year. Mean daily values ranged from 1.9 to 19.4 mg/m^3 with an overall mean of 8.44 mg/m^3.

Mean seasonal ranks of protein and the food index in spring and summer were higher than at other times of the year (Table 4). Chlorophyll *a* values (Table 5) were higher in the summer than at other seasons. Lipid concentrations were highest in spring, whereas carbohydrate concentrations were greatest in fall and winter. Seston DW, PIM and AFDW (Table 5) showed a similar pattern of high fall and spring values.

Of special interest in this study is the relationship among the various organic components of the seston that possibly serve as a source of nutrition for the oyster. The various measures of organic matter include AFDW (volatile organic matter), chlorophyll *a* (phytoplankton biomass), "food" (the

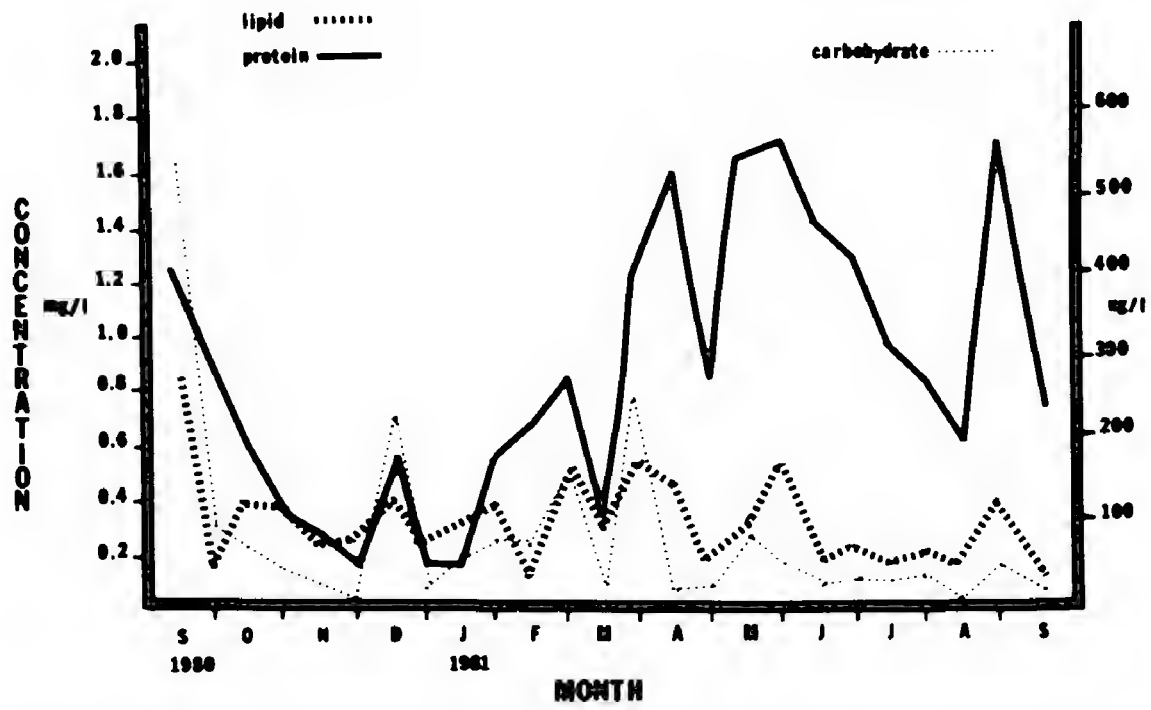

FIG. 3. Semi-monthly measurements of the lipid, carbohydrate and protein concentrations of the seston. Carbohydrate concentration in μg/l; others in mg/l. $N=3$ for each determination.

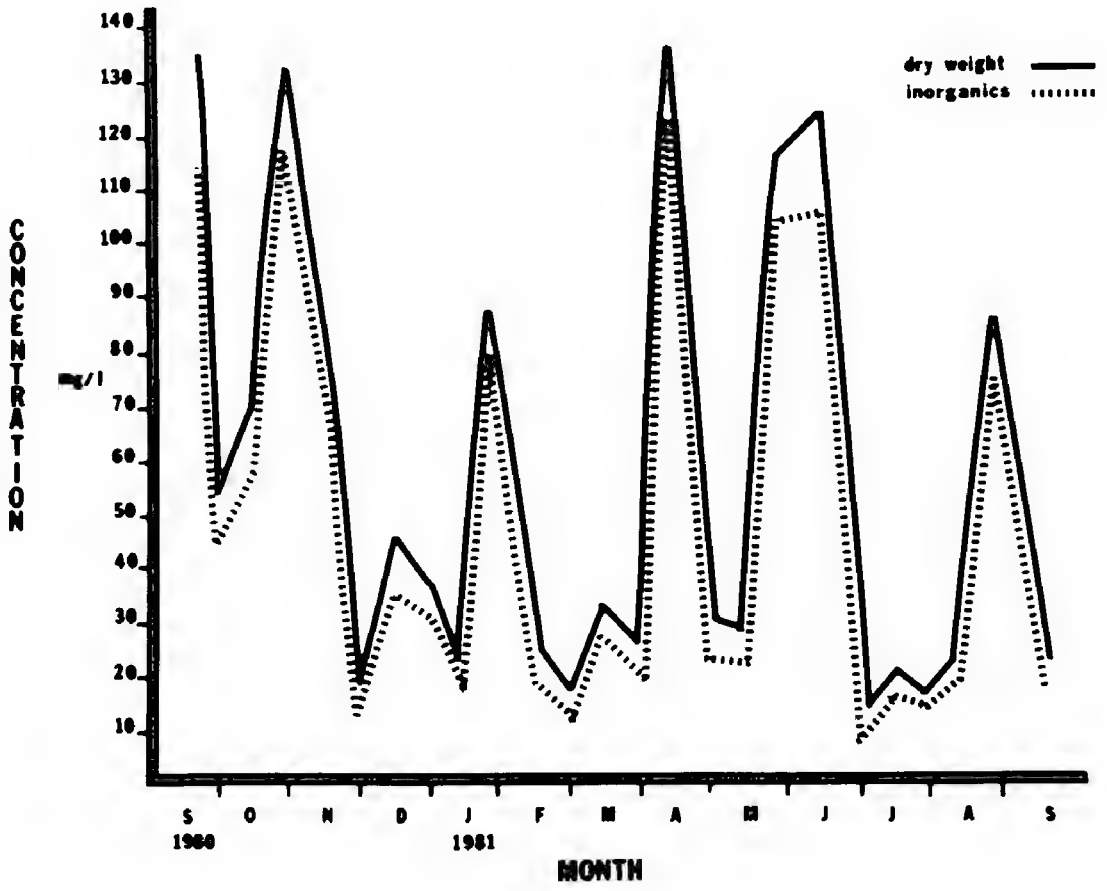

FIG. 4. Semi-monthly estimates of dry and inorganic weight of the seston. $N=3$ for each determination.

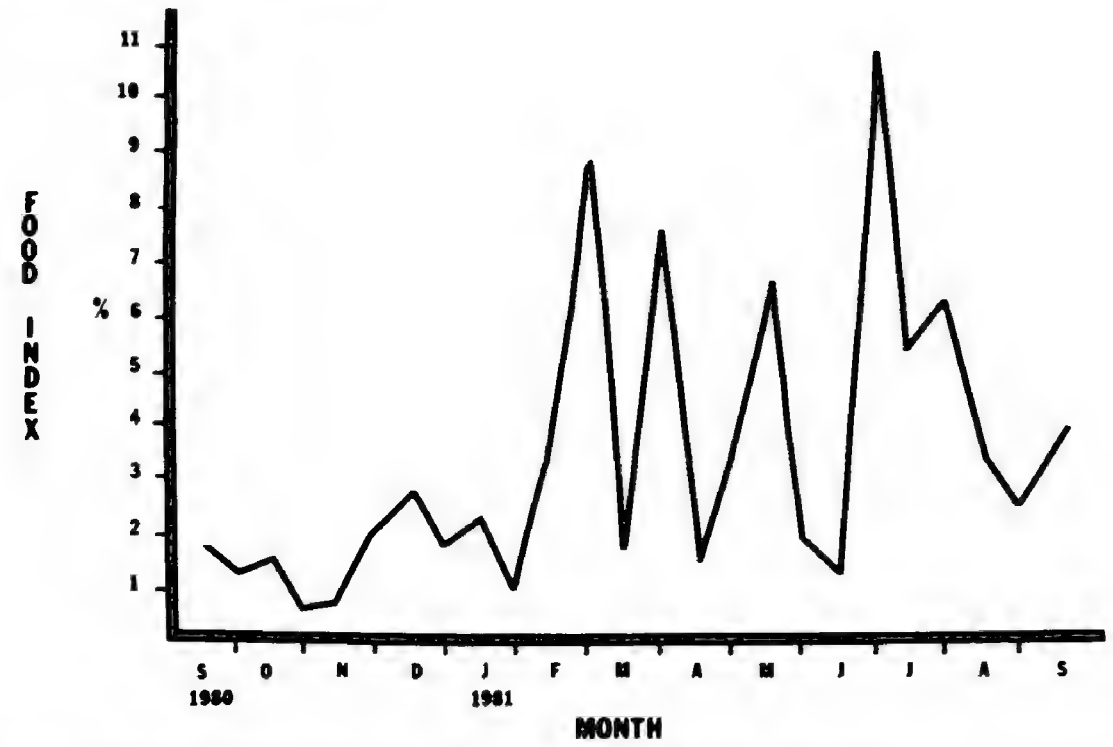

FIG. 5. Semi-monthly food index values. $N=3$ for each determination.

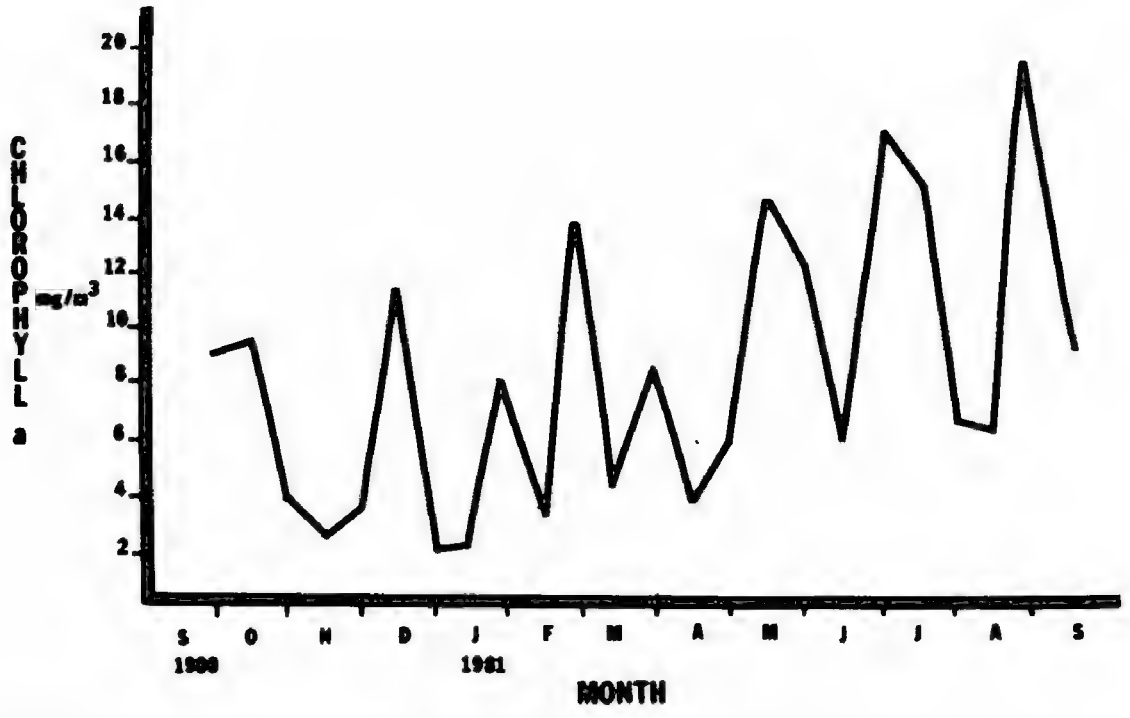

FIG. 6. Semi-monthly chlorophyll *a* concentrations. $N=3$ for each determination.

sum of protein, lipid and carbohydrate) and the food index (the percent "food" in the seston). Correlations between the various measures are presented in Table 6. The AFDW is inversely correlated with the food index; it is weakly correlated with "food." Chlorophyll *a*, "food" and the food index are closely intercorrelated. Phytoplankton organic matter (Table 7) varied from 9.8 to 69.7% of the "food" measure.

DISCUSSION

A significant inverse correlation between wind speed and Secchi depth (Table 2) suggests that at high wind speeds (and therefore elevated wind stresses) more bottom material is resuspended and turbidity increases and thus reduces the secchi depth. Ward (1980) reviewed the hydrography of Gulf estuaries and concluded: "As a general rule, the bay systems of the Gulf of Mexico are meterologically dominated." Wind is a major forcing function in Gulf estuaries; it acts to resuspend bottom sediments and can have a greater effect upon water levels than the relatively feeble astronomical tides. With the resuspension of bottom material, the amount of both inorganic and

TABLE 6

Spearman rank-order correlation coefficients and level of significance for various organic components of the seston possible serving as a source of nutrition for the oyster. AFDW = ash-free dry weight. $N = 75$.

	Chlorophyll *a*	"Food"	Food Index	AFDW
Chlorophyll *a*	-	0.66***	0.46***	0.10
"Food"	-	-	0.44***	0.29*
Food Index	-	-	-	-0.63***
AFDW	-	-	-	-

*$p < 0.05$ **$p < 0.01$ ***$p < 0.001$

organic material in the seston increases. However, inorganic material was always proportionately greater than the AFDW of the resuspended matter.

The three sources of variability in this study are the variability of the analytical tests, variability within sample days and variability between sample days. The variability of the analytical tests for lipid, carbohydrate and protein is relatively small. No independent measures of precision were made for the more standard techniques. It is significant that this work was conducted from a pier, which made sampling possible during rough weather. This study is a record of variability probably not obtainable by sampling from a boat. Despite a fair degree of variability within sample days, the null hypothesis of no difference between days is rejected. Multiple comparisons (Tables 4 and 5) indicate which particular days and seasons are significantly different. For example, high chlorophyll *a* concentrations were found during the summer (and spring, but not significantly so) and the food index was highest in spring and summer. Presumably the nutritional quality of the seston was higher at this time of the year.

The sum of lipid, carbohydrate and protein comprised only a small proportion of the AFDW of the seston. This is consistent with other studies (Parsons and Strickland 1962, Handa, Yanagi, and Matsumaga 1972, Holm-

TABLE 7

Mean chlorophyll *a* values from a sample day ($N=3$), phytoplankton organic matter equivalents and phytoplankton organic matter as a proportion of the L + C + P. Carbon content = chlorophyll *a* × 26 (Parsons *et al.* 1961); organic matter = carbon × 2.14 (Widdows *et al.* 1979). L = lipid concentration, C = carbohydrate concentration, P = protein concentration.

Date	Chlorophyll *a* (µg/ℓ)	Phytoplankton Carbon (µg/ℓ)	Phytoplankton Organic Matter (mg/ℓ)	L+C+P (mg/ℓ)	Phytoplankton Organic Matter as % of L+C+P
09/05/80	14.9	387.4	0.83	2.81	33.0
09/19/80	9.1	236.3	0.51	0.74	68.3
10/3/80	9.6	249.6	0.53	1.09	48.9
10/17/80	3.9	101.4	0.22	0.97	22.4
11/07/80	2.5	65.0	0.14	0.52	27.2
11/21/80	3.9	101.4	0.21	0.38	56.4
12/05/80	11.4	296.4	0.64	1.26	50.4
12/18/80	2.0	52.0	0.11	0.33	33.4
01/03/81	1.9	49.4	0.11	0.54	19.8
01/16/81	8.1	210.6	0.45	1.00	45.0
02/06/81	3.1	80.6	0.17	0.85	20.0
02/19/81	13.6	353.6	0.76	1.57	48.3
03/05/81	4.2	109.2	0.23	0.61	38.1
03/20/81	8.3	215.8	0.46	2.03	22.7
04/03/81	3.7	96.2	0.20	2.07	9.8
04/15/81	5.9	153.4	0.33	1.06	30.1
05/07/81	14.5	377.0	0.80	2.00	40.2
05/21/81	12.1	314.6	0.67	2.29	29.3
06/04/81	5.9	153.4	0.33	1.62	20.4
06/18/81	16.7	434.2	0.93	1.57	59.0
07/02/81	15.0	390.0	0.83	1.19	69.7
07/16/81	6.4	166.4	0.35	1.10	32.3
08/07/81	6.0	156.0	0.34	0.81	42.0
08/20/81	19.4	504.4	1.08	2.19	49.2
09/03/81	9.2	239.2	0.51	0.95	53.6

Hansen 1972, Bowen 1979, Widdows *et al.* 1979). A major portion of the ash-free material is likely to be refractory and probably not suitable as an energy source for filter feeders. The sum of lipid, carbohydrate and protein should prove to be a conservative measure of seston organic matter and (by appropriate conversion factors) seston energy content. The main deficiency of the technique is that it requires three relatively complex analyses per sample (see Newell 1982).

As the food quality of the seston improves, more energy should be available to the oyster. Even under the best of natural conditions, however, the oyster lives in a nutritionally dilute environment. The amount of food, for example, never comprised more than about 11% of the seston (Fig. 5). This compares with a maximum percent food of about 25% from the work of Widdows *et al.* (1979). The food index measure was developed by Widdows *et al.* (1979), who maintain that, in the absence of selective feeding, PIM may simply "dilute" the particulate organic food of filter feeders. However, by actively selecting out organic matter from the seston, a bivalve would be able to ingest organic material in excess of its proportion in the seston.

Selective ingestion of organic material would thus counteract the diluting effect of inorganic material. The work of Loosanoff (1949), Menzel (1955) and Newell and Jordan (1983) suggests that *Crassostrea virginica* does in fact have this ability. Kiøboe, Møhlenberg, and Nøhr (1980) found that *Mytilus edulis* can even benefit from silt concentrations up to 25 mg/l. They later demonstrated (Kiørboe *et al.* 1981) higher growth rates of *M. edulis* at silt concentrations of 5 mg/l than at 0 or 20 mg/l. If the oyster can selectively ingest organic matter, then the food index is not strictly a measure of available food since the oyster can obtain organic matter in excess of its proportion in the seston. The "food" measure is also problematical in that high concentrations of PIM are not likely to be beneficial to the oyster (PIM concentrations ranged from 8.9 to 124.5 mg/l with an average of 46.1 mg/l), and "food" concentrations were generally highest on the most turbid days. However, the "food" measure and the food index are correlated, and both should correlate with oyster production.

The inverse correlations between some of the organic measures are curious results (Table 6). The negative correlation between AFDW and the food index is explainable by the fact that AFDW is so closely and positively correlated with DW; DW is the denominator in the food index values and thus inversely related to the food index. Chlorophyll *a* is closely correlated with the "food" measure whereas AFDW is weakly correlated with "food". Chlorophyll *a* and "food" are probably so closely related because they both likely represent less refractory components of the seston, whereas the ash-free material consists of both refractory and more labile organic constituents. The concentration of AFDW in this shallow portion of the bay was determined largely by the resuspension of bottom material. In contrast, although some benthic diatoms and undegraded chlorophyll *a* were probably resuspended from the bottom, resuspension was not the major factor determining chlorophyll *a* concentrations. If resuspension were the major factor, then chlorophyll *a* should be positively correlated with AFDW (and DW and PIM) and inversely correlated with the food index.

Theoretically, the conversion of chlorophyll *a* data to organic matter provides a method of comparing the relative contribution of phytoplankton to the amount of food present (measured as the sum of lipid, carbohydrate and protein). However, the conversion factors used to change chlorophyll *a* values to carbon equivalents vary greatly from species to species (Parsons *et al.* 1961) and over time (Anita, McAllister, Parsons, Stephens, and Strickland 1963). Widdows *et al.* (1979) used a carbon to chlorophyll *a* ratio of 54. Parsons *et al.* (1961) gave a range in this ratio of 19 to 97. This conversion, however, suggests that (even though chlorophyll *a* and "food" are correlated) non-algal material probably makes an important contribution to the "food" measure.

ACKNOWLEDGMENTS

We wish to thank the Gulf and South Atlantic Fisheries Development Foundation, Inc., and the Texas A&M University Sea Grant Program for their financial support of this research. Howie

Spero provided photographic assistance and Hays Cummins, Jim Nance, and J. P. Schmidt aided in sample collection. Suggestions of Kneeland McNulty and Sam Rogers, especially of a statistical nature, have greatly improved the manuscript. Special thanks to Carolyn Soniat and Marie LeBlanc for their help in preparation of the manuscript.

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Contributions in Marine Science. (1984) Vol. 27:143–158.

THE COMPOSITION AND STANDING STOCK OF MESOPELAGIC MICRONEKTON AT 27°N 86°W IN THE EASTERN GULF OF MEXICO

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ABSTRACT

A series of oblique 0–1000m tows (28) made with 6.5 m^2 Tucker trawls were used to determine the standing stock of micronekton in the eastern Gulf of Mexico in June and September, 1981. The principal groups were semaeostome scyphomedusae, fishes, and crustaceans, which constituted 48.3%, 34.7% and 12.6%, respectively of total micronekton biomass (5371 kg WW/km^2). Semaeostome scyphomedusae, though averaging almost half the WW biomass, were uncommon and occurred in only five tows. *Cyclothone* spp. fishes were the numerically dominant taxa and averaged 34.1% of the total micronekton numbers. Faunal diversity was high with 148 fish and crustacean species being identified.

Diel vertical migration was apparent: 45% of the numbers and 53% of the biomass of micronekton migrated into the upper 40 m at night.

Comparison with what little geographical information is available revealed that micronekton biomass in the upper 1000 m in the eastern Gulf of Mexico is similar to that in waters adjacent to Hawaii but considerably greater than standing stocks in the Caribbean Sea off Puerto Rico.

Accepted 26 March 1984

INTRODUCTION

There have been relatively few assessments of the abundance of micronekton in oceanic habitats. This component of the fauna must be considered in any modeling of pelagic ecosystems because of its importance in regulating plankton dynamics. Our definition of micronekton is based on size alone and includes intermediate sized animals (1.5–20 cm greatest linear dimension) which occupy several trophic levels, *i.e.*, small particle grazers as well as carnivores. The principal taxonomic components are fishes, various kinds of shrimps, some cephalopods, and large gelatinous invertebrates such as tunicates and coelenterates, although the gelatinous groups often are classified as macrozooplankton, (*e.g.*, Biggs, Bidigare, and Smith 1981). Many of these organisms may undergo extensive diel vertical migrations.

The study area was at 27°N 86°W in the eastern Gulf of Mexico, a location we have sampled annually since 1970. This position is usually occupied by Gulf Transitional water which is found at the eastern boundary of the Gulf Loop Current. Zooplankton standing stock in the upper 1000 m at this location has been estimated at 1.2 gDW/m² which is in the range reported for oligotrophic boundary currents (Vinogradov 1970, Hopkins 1982, this study). No seasonal information on phytoplankton is available for this particular location but extrapolation from El-Sayed's (1972) data and our own *in situ* C^{14} results (unpublished) indicate an annual production of less than 50 gC/m², which is also indicative of an oligotrophic regime.

Expendable bathythermograph traces (Fig. 1) from 27°N 86°W show

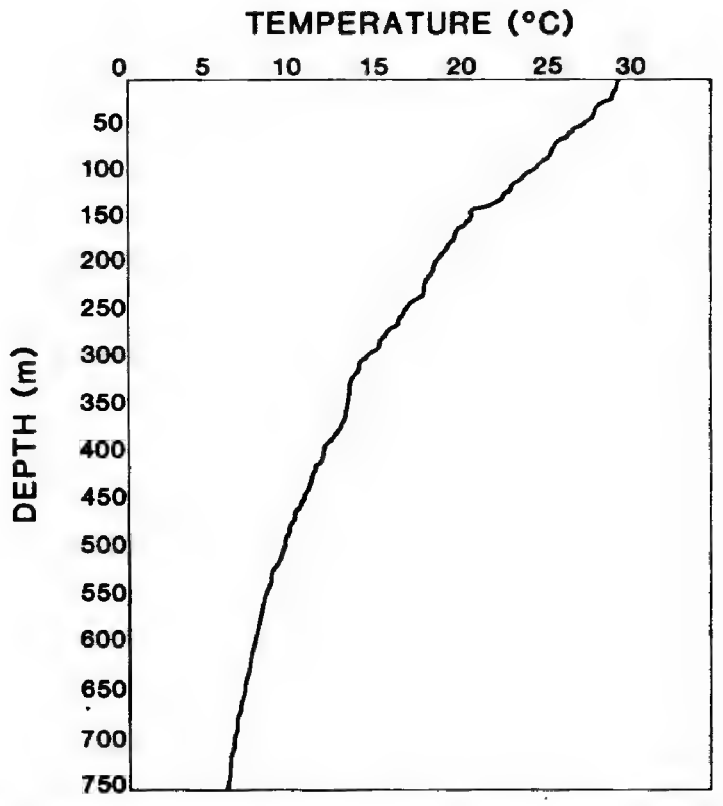

FIG. 1. Bathythermograph trace representing a compilation of data from six XBT traces taken during the summer of 1981 at 27°N 86°W.

summer surface temperatures in 1981 to be 28–30°C, a mixed layer extending from the surface to 30 to 50 m, and the steepest part of the thermocline occurring from 50 to 150 m. The water column is well oxygenated with a minimum of 2.7–2.9 ml/l (Hopkins, unpublished data; see also Nowlin 1971) between 400 and 500 m. This hydrographic pattern is characteristic of vertically structured oligotrophic waters at tropical-subtropical latitudes (McGowan 1974, Longhurst 1976). Consequently, the present information should have general applicability.

METHODS

Micronekton were collected in two series of oblique tows (0–400 m and 0–1000 m, Table 1) with a Tucker trawl, 6.5 m² in mouth area, during June and September, 1981. The main net was

TABLE 1

Collection data for oblique biomass tows made on cruises B-8120 (June, 1981) and B-8126 (September, 1981) to 27°N 86°W, N,D,T, represent night, day, and twilight hauls (See Methods for sunrise, sunset times).

Tow	Date	Local Time	Diel Period	Tow duration (min)	Maximum depth (m)	Estimated filtered ($10^4 m^3$)
B521	6/27-28	2115-0115	N	240	910	5.20
B522	6/28	0448-0945	D	297	1170	3.30
B524	6/28	1123-1648	D	325	1000	3.23
B526	9/2	0928-1330	D	242	1000	4.86
B527	9/2	1400-1534	D	94	400	2.00
B528	9/2	1719-2115	T	236	1100	4.58
B529	9/3	0050-0223	N	93	400	1.94
B530	9/3	0242-0615	T	213	1000	4.45
B531	9/3	0649-0900	D	131	400	3.59
B532	9/3	0929-1210	D	161	1000	3.11
B533	9/3	1300-1440	D	100	400	2.68
B534	9/3	1522-1930	D	248	1000	5.57
B535	9/3	1955-2130	N	95	400	2.23
B536	9/3	2205-2341	N	96	400	2.09
B537	9/4	0010-0515	N	305	1000	6.87
B538	9/4	0539-1002	D	266	1000	6.68
B539	9/4	1030-1235	D	125	400	3.03
B540	9/4	1300-1705	D	245	1000	5.36
B541	9/4	1740-2200	T	260	1000	5.81
B542	9/4-5	2250-0020	N	90	400	1.98
B543	9/5	0045-0418	N	213	1000	3.99
B544	9/5	0517-0923	D	246	1000	5.97
B545	9/5	1015-1203	D	108	400	2.67
B546	9/5	1235-1626	D	231	1000	5.68
B547	9/5	1657-2100	T	243	1000	5.50
B548	9/5-6	2150-0255	N	305	1000	7.10
B550	9/6	0510-0824	D	194	1000	3.43
B551	9/6	0855-1330	D	275	1000	5.69

1.8 × 3.6 m in mouth dimensions and was constructed of 4 mm mesh that tapered down to a 0.5 m plankton net of 1 mm mesh. The cod end net (bucket) was also 1 mm mesh. The bottom spreader bar was loaded with 180 kg of lead and when the trawl was towed just beneath the surface at average towing speeds, observations indicated the angle of the net mouth varied 30–35° from the vertical. The resulting reduction of effective fishing area of the trawl mouth was included in calculations of filtration volumes. Volume of water filtered was measured with a set of dial-type propeller flowmeters mounted on the top spreader bar. A filtration efficiency of 100% was assumed.

The trawl was fished from conducting cable that allowed depth to be accurately monitored with a depth transducer-deck readout system. Traces of the path of the trawl through the water were also obtained with a time-depth recorder attached to the top spreader bar. The trawl was towed open at approximately two knots, with wire being paid out at 10 m/min and retrieved at

15 m/min. This procedure resulted in oblique tows which fished on ascent and descent. While this strategy resulted in the trawl moving more slowly through the water on descent than ascent, this was balanced to some degree by the fact that effective fishing area was greater on descent than ascent. Filtration rate (volume filtered/tow duration) varied from 1.7 to 4.5 m^3/sec but rates for two-thirds of the tows were within ± 18% of the mean rate of 3.6 m^3/sec. Consequently, all tows were treated as comparable. Also, the three June, 1981 tows [B521, B522, B524] were included with the September, 1981 group because total numbers adjusted to a km^2 of sea surface were all within 10% of the September mean values and the same dominant species occurred in each of these trawls as in our September catches. Sunrise and sunset for the June 27–28 sampling interval were 0508 and 1859 hours, respectively. For the midday of the September 2–6 trawling period these times were 0540 and 1819 hours. Sunrise or sunset occurred during five of the 28 tows, with all but one, B522, being considered as twilight tows in our data set. Tow B522 was treated as a daylight collection because most of the five-hour haul occurred during daylight with sunrise occurring only twenty minutes after launching.

Micronekton samples were stored in 10% formalin buffered with borax. Very large scyphomedusae were weighed to the nearest gram aboard ship then discarded. Sections were removed from some individuals for dry weight and ash weight analyses. Micronekton samples were subsequently transferred to 50% isopropyl alcohol for storage. Analysis involved identifying micronekton to species, taking length measurements, then obtaining net weights (± 1 mg) of each individual after removal of excess surface fluid. Weights of animals stored in alcohol were adjusted to an estimated fresh weight through comparisons of regressions of weight on size for fresh and alcohol stored material. All dry weights were of organisms dried to a constant weight at 60°C. Ash content was determined by combustion of dried material at 450°C for at least 24 hours. Both dry and ash weights were determined to the nearest 0.01 mg.

Abundance and biomass of micronektonic species were expressed as numbers of individuals and kilograms wet weight per square kilometer of sea surfacc, respectively. They were calculated by estimating from flowmeters the volumes of water filtered, in cubic meters, by standardizing the number and biomass of each species in trawl catches to a cubic meter, and by then multiplying by either 0.4×10^9 or 1×10^9, which respectively, represent the volumes (in m^3) of water in the upper 400 m and 1000 m under a square kilometer of sea surface.

The species of micronekton collected in our 0–1000 m trawls were assigned to the following taxonomic groups in order to assess general patterns: Myctophidae; *Cyclothone* (Gonostomatidae); other Gonostomatidae (= all other non-*Cyclothone* genera in this family, *sensu* Grey 1964); Sternoptychidae (*sensu* Baird 1971); other Stomiatoidei; leptocephalus larvae (mostly Congridae and Ophichthidae); miscellaneous fishes; Caridea; Penaeidea; Euphausiacea; Mysidacea; miscellaneous crustaceans; Coelenterata; Tunicata; Cephalopoda; and miscellaneous invertebrates.

Zooplankton were collected for biomass analysis with a 66 × 66 cm square-mouth (0.44 m^2 mouth area), 165 μ mesh net mounted in the mouth of the Tucker trawl (see Hopkins and Baird 1975). Volume filtered was measured with a dial-type propeller meter suspended in the mouth of the plankton net. Each collection was quantitatively halved aboard ship. One portion was preserved in buffered formalin; the other half was drained and gently blotted of excess water, frozen aboard ship, and then weighed (wet) in the laboratory to the nearest milligram. Prior to splitting the sample all micronekton were removed and added to the trawl catch. The dry and ash weights of the frozen half of the sample were determined by the same procedure as for the individual organisms. Student's *t*-tests were used to compare means of day and night catches for individual groups and the total samples; modification of the information index, $\bar{D}$ (see Travers 1971), was used as a measure of trawl catch diversity.

RESULTS

The species of micronekton taken in the 0–1000 m oblique trawls are listed in the appendix and abundance of major categories in terms of

numbers and biomass per square kilometer of sea surface are in Tables 2 and 3, respectively. A comparison of the percentage contribution of each

TABLE 2

Abundance of micronekton in the upper 1000 m per k^2 of sea surface. * = either day or night value significantly larger (*t*-test: $P<0.05$). Standard deviations of X in parentheses.

Micronekton category	No. ($x10^3$)/km^2 Day (11 tows)	Twilight (4 tows)	Night (4 tows)
Myctophidae	487(193)	643(311)	822(249)*
Cyclothone (Gonostomatidae)	2191(282)	1941(763)	1961(456)
Other Gonostomatidae	121(72)	203(97)	206(48)*
Sternoptychidae	205(80)*	149(58)	151(27)
Other Stomiatoidei	50(33)	49(111)	79(29)
Leptocephalus larvae	110(76)	157(5)	222(139)
Miscellaneous fishes	153(115)	162(12)	246(100)
Caridea	246(79)	226(72)	219(28)
Penaeidea	804(294)	774(276)	1142(349)
Euphausiacea	247(110)	228(45)	316(244)
Mysidacea	245(80)	195(90)	215(30)
Miscellaneous crustacea	40(90)*	42(38)	44(40)
Coelenterata[1]	59(50)	43(33)	26(6)
Tunicata	-	4(-)	10(-)
Cephalopoda	29(20)	18(25)	38(25)
Miscellaneous invertebrates	144(76)*	79(64)	64(31)
Totals	5131(627)	4904(1267)	5761(373)*

[1] exclusive of siphonophores

category to abundance and biomass is shown in Figure 2.

The most abundant micronekton were the *Cyclothone* fishes which constituted 34.1% of the numbers of micronekton in the upper 1000 m. *Cyclothone pallida* was the most prevalent species and constituted over half the *Cylothone* population. Penaeid shrimps ranked second numerically; *Gennadas valens* alone accounted for 62% of this group. Myctophid fishes were third; *Ceratoscopelus warmingii, Diaphus dumerilii, Lampanyctus alatus* and *Lepidophanes guentheri* totalled 53% of the lanternfish population.

Large tunicates, *e.g.*, salps, and siphonophore were relatively uncommon in our catches. This, in part, may have been due to losses by fragmentation and/or extrusion through the trawl meshes. Among the miscellaneous invertebrates, losses through fragmentation undoubtedly occurred as well in polychaetes (*e.g.*, Alciopidae) and ctenophores. Cephalopods were also uncommon, possibly due to net avoidance. Semaeostome scyphomedusae

TABLE 3

Biomass of micronekton in the upper 1000 m per km² of sea surface. * = either night or day values significantly larger. (*t*-test; $P<0.05$). Standard deviation in parenthesis.

Micronekton Category	Day (11 Tows) WW	Day (11 Tows) AFDW	Twilight (4 Tows) WW	Twilight (4 Tows) AFDW	Night (4 Tows) WW	Night (4 Tows) AFDW
Myctophidae	248(139)	40.7	330(235)	54.1	397(187)	65.1
Cyclothone (Gonostomatidae)	239(38)	38.7	214(78)	34.7	232(58)	37.6
Other Gonostomatidae	47(52)	6.2	143(107)	19.0	354(263)*	47.1
Sternoptychidae	110(78)	14.1	142(85)	18.2	124(78)	15.9
Other Stomiatoidei	64(96)	5.6	213(292)	18.7	83(55)	7.3
Leptocephalus larvae	32(14)	6.0	58(44)	11.0	98(94)	18.5
Miscellaneous fishes	153(156)	43.0	245(202)	68.8	174(327)	48.9
Caridea	236(124)	44.1	227(140)	42.4	262(102)	49.0
Penaeidea	298(110)	50.3	268(90)	45.3	454(100)*	76.7
Euphausiacea	36(16)	7.2	37(13)	7.4	49(37)	9.8
Mysidacea	54(23)	11.2	41(24)	8.4	62(45)	12.8
Miscellaneous crustacea	13(25)*	0.7	11(10)	0.6	23(22)	1.2
Coelenterata (semaeostomes excluded)	254(277)*	3.7	235(294)	3.4	70(54)	1.0
Semaeostome scyphomedusae	8047(-)	98.9	392(-)	4.7	- (-)	-
Tunicata	261(-)	0.4	16(-)	0.2	5 (-)	0.1
Cephalopoda	131(13)	1.2	96(184)	8.6	117(159)	10.7
Miscellaneous invertebrates	144(253)	13.9	34(32)	3.3	54(58)	5.2
Totals	10014(11264)*	385.9	2702(898)	348.8	2558(231)	406.9
Totals (without semaeostome scyphomedusae)	1967(496)	287.0	2310(636)	344.1	2558(231)*	406.9
Zooplankton[1] (g/m²)	9.64(5.15)	0.53	12.41(12.93)	0.61	7.68(7.06)	0.51

were one of the rarest organisms in our catches, yet relative to collections made at this site in other years and seasons, the number collected in this study was large.

The biomass results showed somewhat different patterns than did numerical abundance. Semaeostome scyphomedusae were ranked first, contributing nearly half of the total micronekton biomass in the upper 1000 m. However, these occurred in only five tows, four day hauls (B526, B532, B538, B550) and one twilight haul (B541). Myctophids ranked second and other Gonostomatidae ranked third. Penaeid shrimps, second in numerical abundance, were fourth in biomass contribution. *Cyclothone* fishes, the numerically dominant category, was only fifth in terms of biomass. In terms of dry weight, coelenterates, while averaging nearly half the total sample wet weight, were only 6.8% of total AFDW. Conversely, fishes and crustaceans, which averaged 34.7% and 12.6%, respectively, of total sample wet weight, increased in importance to 64.7% and 25.6% of total AFDW.

Micronekton Category	No. ($x10^3$)/km^2	Biomass Parameter WW kg/km^2	AFDW kg/km^2
Myctophidae	(15.2)	(10.0)	(18.8)
Cyclothone	(34.1)	(5.0)	(9.4)
(Gonostomatidae)			
Other Gonostomatidae	(3.8)	(7.2)	(10.9)
Sternoptychidae	(2.7)	(2.1)	(3.0)
Other Stomiatoidei	(1.5)	(4.3)	(4.3)
Leptocephalus larvae	(3.7)	(1.4)	(3.1)
Miscellaneous fishes	(4.1)	(4.7)	(15.2)
Caridea	(3.9)	(4.0)	(8.5)
Penaeidea	(19.6)	(6.8)	(13.2)
Euphausiacea	(5.3)	(0.7)	(1.6)
Mysidacea	(3.4)	(0.9)	(2.1)
Miscellaneous crustacea	(0.6)	(0.2)	(0.2)
Coelenterata	(0.4)	(1.7)	(0.3)
(semaostomes excluded)			
Semaostome scyphomedusae	(0.1)	(48.3)	(6.8)
Tunicata	(0.1)	(0.3)	(<0.1)
Cephalopoda	(0.5)	(1.5)	(1.5)
Miscellaneous invertebrates	(1.0)	(0.9)	(1.0)
TOTALS (PERCENT)	100.0	100.0	100.0
TOTALS (PARAMETER)	5706	6388	557

FIG. 2. A comparison of the percentage contribution (values in parentheses) of each micronekton category to the total abundance and biomass. Semaeostome values estimated from day and twilight values.

This series of collections (Tables 2 and 3) indicated an uneven day-night distribution of the catch. Significantly ($P \pm 0.05$) more micronekton was captured at night than during the day, if semaeostome scyphomedusae are excluded from consideration. More myctophids and non-*Cyclothone* gonostomatids were taken at night, along with a greater biomass of the latter group and of penaeid shrimps. Conversely, several groups that were more abundant in our day catches included the Sternoptychidae and the catch-all categories of miscellaneous crustaceans and miscellaneous invertebrates. If semaeostome scyphomedusae are included in the averages, then total day

biomass exceeded that for night by a factor of nearly four. The twilight sample biomass (semaeostome scyphomedusae excluded) was intermediate between day and night averages, whereas the average number of organisms caught during this period was slightly lower than in either the day or night.

To gauge the extent of vertical migration of micronekton in the eastern Gulf, a series of day and night oblique tows were made to a depth of 0–400 m. This depth was selected on the basis of DSL patterns in the eastern Gulf (Baird and Wilson 1977) and because our results would be directly comparable to the earlier study of Maynard, Riggs, and Waters (1975) in waters off Hawaii.

The data in Table 4 show that both numbers and biomass of total micro-

TABLE 4

Diel variations in the abundance and biomass of micronekton in the upper 400 m at 27°n 86°W. Values are averages based on four day tows and five night tows.

Micronekton Category	No. ($\times 10^3$)/km²		Kg WW/km²	
	Day	Night	Day	Night
Myctophidae	11	866	3	639
Cyclothone (Gonostomatidae)	152	219	17	322
Other Gonostomatidae	54	194	6	356
Sternoptychidae	10	53	2	28
Other Stomiatoidei	6	50	3	113
Leptocephalus larvae	112	293	58	70
Miscellaneous fishes	28	260	5	132
Caridea	3	112	1	68
Penaeidea	3	711	1	261
Euphausiacea	12	160	1	28
Mysidacea	3	---	1	---
Miscellaneous crustacea	---	15	---	7
Coelenterata	67	4	14166	10
Tunicata	4	5	11	5
Cephalopoda	3	24	2	21
Miscellaneous invertebrates	47	51	31	44
Total	515	3017	14305	1975
Biomass Total (less semaeostome scyphomedusae)			219	1975

nekton were 6 to 7 times greater in our night 0–400 m catches, if large scyphomedusae are excluded. Daytime catches of large coelenterates notwithstanding, it is apparent that organisms in most categories were taken in greater quantities at night than day in the upper 400 m. The myctophid fishes and penaeid shrimps accounted for a major fraction of the nocturnal

increase in micronekton numbers and myctophids, penaeids and gonostomatids accounted for much of the nighttime biomass increase. Daylight numbers of fishes and crustaceans in collections from the upper 400 m were only 10% and 1%, respectively, of the total numbers for these groups in the 0–1000 m zone, whereas at night these percentages increased to 52% and 53%, respectively. Comparable increases occurred in micronekton biomass.

DISCUSSION

Total standing stock of micronekton in summer in the upper 1000 m in the eastern Gulf of Mexico at 27°N 86°W was estimated to be 2558 kg WW/km^2. This determination was based on nighttime collections and is exclusive of semaeostome scyphomedusae. If the latter are added, the standing stock doubles (5371 kg WW/km^2). Ash free dry weight with and without the Semaeostomeae is 577 and 519 kg AFDW/km^2, respectively, which demonstrates the reduced importance of these large organisms in terms of dry organic weight. Also, semaeostome medusae were numerically rare in comparison to organisms in other major biomass groups (*e.g.*, fishes and shrimps) and appeared patchily in our trawl series. Thus, their impact on ecosystem trophic dynamics despite their large individual bulk, is presumably areally quite localized. However, recent open ocean scuba diving (Harbison, Madin, and Swanberg 1978, Biggs *et al.* 1981), has revealed the significant abundance of other large gelatinous animals such as siphonophores and ctenophores in the epipelagic zone at tropical-subtropical latitudes. These taxa did not rank high in the present set of collections. They may have been seriously underestimated with our trawling techniques however, because these organisms are fragile and easily fragmented.

Few comparable data on micronekton are available, the Gjøsaeter and Kawaguchi (1980) review notwithstanding. The only other results based on roughly similar analyses are those of Maynard *et al.* (1975) from waters adjacent to Hawaii and of Hopkins (1981) from off southeastern Puerto Rico. As indicated in Table 5, Gulf of Mexico standing stock is intermediate at half the Hawaiian and double the Puerto Rican value. However, if semaeostome scyphomedusae biomass is included, the Gulf estimate exceeds that for waters off Hawaii. The regional variation apparent here and in the subsequent comparisons undoubtedly is related to differences in collection methods as well as to variations in levels of natural abundance. Tucker trawls were the collecting gear in the Gulf of Mexico and Puerto Rican investigations whereas an Isaacs-Kidd trawl towed at twice the speed was used off Hawaii. Also, in the former pair of studies only the upper 1000 m was sampled while off Hawaii the depth range sampled was 0–1200 m. Given these potential sources of variation, then the difference between the Gulf and Hawaiian standing stock estimates does not seem large. However, both of these standing stocks are about 2 to 4 times that determined for waters off Puerto Rico. These three sampling locations are at relatively low latitudes 18–27°N, and have annual productivities estimates at 50 gC/m^2 or less. Zoo-

TABLE 5

Comparison of biological characteristics in the 0–1000 m zone in different geographical areas.

	Gulf of Mexico (27°N 86°W)	Caribbean off Puerto Rico (17°57'N 65°48'W)	Pacific off Hawaii (21°22'N 158°22'W)
Micronekton biomass (kg WW/km²)	2558 5371[5]	1280[1]	4940[3]
Zooplankton biomass (kg WW/km²), 0–200 m zone	5800[4]	700[2]	2600
Micronekton major group diversity (D; (Travers, 1971)	3.54	3.64	3.67
Fish: crustacean biomass ratio	2.7:1	1.8:1	2.2:1
Caridean:penaeid biomass ratio	0.6:1	1.7:1	1.6:1

[1] All data in this column, except that for zooplankton, from Hopkins (1981).

[2] Modified from Michel (1981).

[3] All data in this column derived from Maynard *et al.* (1975); zooplankton value from Nakamura cited in Maynard *et al.* (1975).

[4] From Hopkins (1982) and present study. The present zooplankton data ($\bar{X}$ all tows) was multiplied by 0.59 to obtain the fraction of the total 0–1000 m zooplankton biomass in the upper 200 m at 27°N 86°W. This conversion factor was derived from the discrete depth haul, results published earlier (Hopkins, 1982)

[5] Nighttime biomass total with average of day and twilight value for semaeostome scyphomedusae added in.

plankton standing crop at the Gulf location appears to be the highest, though both the Hawaiian and Gulf zooplankton biomass values exceed that for the Puerto Rican site by about 4 and 8 times, respectively

These three tropical-subtropical locations show predictably high faunal diversity within the micronekton (see Clarke 1973, 1974; Walters 1976; Backus, Craddock, Haedrich, and Robison 1977; Hopkins 1981); their diversity indices, based on the major taxonomic categories as listed in Tables 2 and 3, for the three areas are quite similar. However, the structure of the food web in these oceanic regions is not identical as indicated by differences in the ratios of major micronekton categories (Table 5). For example, the fish to crustacean biomass quotients range from 1.8 to 2.7, and the caridean:penaeid biomass ratios show marked regional differences. Carideans contribute proportionately the most to shrimp biomass in Puerto Rican and Hawaiian waters but not in the Eastern Gulf.

Maynard *et al.* (1975) found in their study off Hawaii that 43% of the numbers and 47% of the biomass of micronekton migrates into the upper 400 m at night. In the Gulf the percentages are comparable, 45% and 53%, respectively. As in Hawaiian waters, most of the vertical migration into the upper 400 m is attributable to fishes and shrimps, particularly the Myc-

tophidae, other Gonostomatidae, and Penaeidea (Table 5; Maynard *et al.* 1975, Table 7). If diel vertical migration is largely a feeding migration, as Marshall (1971) suggests, then the grazing pressure of mesopelagic micronekton on their plankton resource is not distributed uniformly, or randomly for that matter, in terms of time and space in the 0–1000 m zone. On the basis of our sampling and other studies in tropical-subtropical latitudes (*e.g.*, Badcock 1970, Clarke 1973, Badcock and Merrett 1976, Hopkins 1981, Hopkins 1982), it is principally the myctophids that concentrate in the upper 200 m at night and it is in the upper 200 m that the greatest impact on zooplankton from micronekton predation would be predicted. It should be cautioned that the observed diel increase at night in the upper 400 m, at least in the present study, stems from a combination of factors which include genuine vertical migrations as well as patchy distributions and avoidance of our collecting gear, especially during the day. On the basis of deep scattering layer observations (Baird and Wilson 1977) in the eastern Gulf, however, there can be little doubt that much of this variation in the upper 400 m results from the diel migrations of micronekton.

ACKNOWLEDGMENTS

Ths research was supported by the National Science Foundation under grant OCE 75-1384. Shiptime on the RV BELLOWS was funded by the Florida Institute of Oceanography.

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APPENDIX

Micronekton taxa collected in the 0-1000 m oblique hauls. Numbers represent total numbers captured.

MYCTOPHIDAE	
Myctophidae (unident.)	15
Benthosema suborbitale	30
Bolinichthys photothorax	2
Bolinichthys supralateralis	2
Centrobranchus nigroocellatus	1
Ceratoscopelus warmingii	88
Diaphus brachycephalus	4
Diaphus dumerilii	78
Diaphus luetleni	2
Diaphus lucidus	7
Diaphus mollis	25
Diaphus rafinesquii	12
Diaphus splendidus	2
Diaphus taaningi	1
Diaphus termophilus	1
Diogenichthys atlanticus	9
Gonichthys cocco	2
Hygophum benoiti	42
Hygophum taaningi	13
Hygophum reinhardtii	2
Lampadena luminosa	3
Lampanyctus alatus	72
Lampanyctus ater	6
Lampanyctus cuprarius	2
Lampanyctus lineatus	17
Lampanyctus nobilis	3
Lampanyctus tenuiformis	4
Lepidophanes guentheri	66
Lobianchia gemellarii	2
Myctophum affine	27
Myctophum nitidulum	1
Notolychnus valdiviae	26
Notoscopelus caudispinosus	1
Notoscopelus resplendens	9
Taaningichthys bathyphilus	1

CYCLOTHONE (GONOSTOMATIDAE)	
Cyclothone acclinidens	296
Cyclothone alba	132
Cyclothone braueri	127
Cyclothonemicrodon	16
Cyclothone obscura	10
Cyclothone pallida	1080
Cyclothone pseudopallida	358
Cyclothone sp.	37

OTHER GONOSTOMATIDAE	
Bonapartia pedaliota	1
Gonostoma atlanticum	1
Gonostoma elongatum	39
Margrethia obtusirostra	1
Maurolicus muelleri	1
Pollichthys mauli	3
Valenciennellus tripunctulatus	90
Vinciguerria nimbaria	8
Vinciguerria poweriae	9

STERNOPTYCHIDAE	
Argyropelecus aculeatus	21
Argyropelecus affinis	1
Argyropelecus gigas	1
Argyropelecus hemigymnus	50
Argyropelecus sladeni	3
Sternoptyx diaphana	51
Sternoptyx pseudobscura	43
Polyipnus asteroides	1
Polyipnus polli	4
Polyipnus sp.	4

OTHER STOMIATOIDEI	
Astronesthidae	

Astronesthes macropogon	1
Astronesthes indicus	1
Astronesthes niger	2
Astronesthes similis	1
Chauliodontidae	
Chauliodus sloani	15
Malacosteidae	
Aristostomias grimaldii	1
Aristostomias tittmanni	1
Aristostomias sp.	5
Photostomias guernei	12
Melanostomiatidae	
Bathyphilus nigerrimus	1
Bathophilus pawneei	3
Bathophilus sp.	1
Leptostomias bilobatus	1
Melanostomias melanops	1
Melanostomias valdiviae	1
Stomiatidae	
Stomias affinis	8

LEPTOCEPHALUS LARVAE

Leptocephalus larvae	142

MISCELLANEOUS FISHES

Alepocephalidae	
Photostylus pycnopterus	1
Balistidae	2
Bathylagidae	
Bathylagus bericoides	1
Bathylagus compsus	8
Bergmacerotidae	
Bergmaceros atlanticus	8
Brotulidae	3
Carangidae	
Decapterus punctatus	1
Selar crumenophthalmus	2
Ceratioidei (unident.)	4
Cetomimidae	1
Cheilodipteridae	1
Chiasmodontidae	
Dysalotus alcocki	1
Kali normanni	1
Pseudoscopelus altipinnis	1
Evermannellidae	
Coccorella atlantica	2
Odontostomops normalops	1
Gadidae	1
Linophrynidae	1
Melamphaidae (unident.)	1
Melamphaes longivelis	1
Melamphaes typhlops	7
Melamphaes sp.	5
Poromitra crassiceps	2
Scopeloberyx opisthopterus	7
Scopeloberyx robustus	3
Scopelogadus mizolepis	1
Moridae	
Melanonus sp.	3
Nemichthidae (unident.)	1
Avocettina infans	4

MISCELLANEOUS FISHES

Omosudidae	
Omosudis lowei	5
Oneiroididae	1
Paralepididae	2
Rondoletiidae	
Rondoletia bicolor	1
Scopelarchidae	
Scopelarchus analis	2
Searsiidae	1

Serrivomeridae	
Serrivomer brevidentatus	1
Other fishes (unident.) (damaged and neretic larvae)	85
CARIDEA	
Caridea (unident.)	13
Breseliidae	
Lucaya bigelowi	7
Oplophoridae	
Acanthephyra acutifrons	4
Acanthephyra curtirostris	25
Acanthephyra purpurea	68
Acanthephyra stylorostrata	4
Acanthephyra acanthitelsonis	19
Ephyrina benedicti	2
Meningodora marptocheles	1
Meningodora mollis	2
Meningodora vesca	13
Notostomus elegans	1
Notostomus perlatus	4
Notostomus westergreni	6
Oplophorus spinosus	1
Systellaspis debilis	34
Pandalidae	
Parapandalus richardi	17
Pasiphaeidae	
Parapasiphaea sulcatifrons	4
Parapasiphaea sp.	2
Pasiphaea merriami	5
Pasiphaea sp.	13
PENAEIDEA	
Penaeidae (unident.)	1
Bentheogennema intermedia	30
Gennadas bouvieri	9
Gennadas capensis	71
Gennadas scutatus	5
Gennadas valens	503
Sergestidae (unident.)	7
Sergestes armatus	5
Sergestes corniculum	57
Sergestes filictum	16
Sergestes grandis	3
Sergestes japonicus	2
Sergestes pectinatus	2
Sergestes robustus	35
Sergestes sargassi	7
Sergestes splendens	51
Sergestes talismani	2
Sergestes vigilax	2
Sergestes atlanticus	6
EUPHAUSIACEA	
Bentheuphausiidae	
Bentheuphausia amblyops	6
Euphausiidae (unident.)	4
Euphausia gibboides	1
Nematobrachion boopis	48
Nematobrachion flexipes	1
Nematobrachion sexspinosus	6
Stylocheiron maximum	12
Thysanopoda egregia	1
Thysanopoda monocantha	53
Thysanopoda obtusifrons	1
Thysanopoda orientalis	49
Thysanopoda pectinata	49
Thysanopoda tricuspidata	14
MYSIDACEA	
Eucopiidae	
Eucopia australis	40
Eucopia grimaldii	1
Eucopia sculpticauda	81
Eucopia unguiculata	92
Eucopia sp.	6
Lophogastridae	
Gnathophausia ingens	4

Gennadas sp.	9
Funchalia villosa	2
Stomatopoda	25
Palinuridae (larvae)	12
COELENTERATA	
Hydromedusae (unident.)	2
Aequoridae	12
Semaeostomeae	11
Periphyllidae	
Periphylla periphylla	11
Atollidae	
Atolla sp.	5
TUNICATA	
Salpidae	4
Prysomidae	1
MISCELLANEOUS CRUSTACEANS	
Amphipoda	25
CEPHALOPODA	
Cephalopoda (unident.)	5
Bolitaenidae	1
Cranchiidae	9
Grimalditeuthidae	1
Lycoteuthidae	5
Mastigoteuthidae	2
Vampyroteuthidae	1
Octopoda	2
MISCELLANEOUS INVERTEBRATES	
Ctenophora	52
Polychaeta	7
Pteropoda	9
Heteropoda	47

Contributions in Marine Science. (1984) Vol. 27:159–167.

SELECTION FOR BROWN SHRIMP, *PENAEUS AZTECUS,* AS PREY BY THE SPOTTED SEATROUT, *CYNOSCION NEBULOSUS*

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ABSTRACT

Prey selection by spotted seatrout (*Cynoscion nebulosus*) (160–210 mm TL) was examined in the laboratory to provide information on predator-prey interactions in estuarine systems. In tanks without an accessible substrate for burrowing, seatrout fed exclusively on brown shrimp (*Penaeus aztecus*) and did not eat juvenile spot (*Leiostomus xanthurus*). In tanks with a sand substrate, some spot were eaten, but selection for brown shrimp was still significant. Burrowing by shrimp into the substrate apparently reduced their availability to the predators. Prey ranged in size from 59 to 85 mm (TL), and seatrout selected shrimp and fish within the lower half of this size range. In a separate feeding trial, spotted seatrout selected juvenile spot over juvenile pinfish (*Lagodon rhomboides*).

Accepted 6 April 1984

INTRODUCTION

The occurrence of penaeid shrimp in stomach contents of predatory estuarine fishes indicates that predation is a potentially important component of natural mortality of shrimp in estuaries. Many studies have identified the spotted seatrout (*Cynoscion nebulosus*) as a major predator of penaeid shrimp (Pearson 1928, Knapp 1949, Miles 1950, Kemp 1950, Moody 1950, Stewart 1961, Seagle 1969). In contrast, other studies have shown that juvenile fish are abundant in the stomachs of spotted seatrout, and that penaeid shrimp are a relatively minor dietary component although present in samples of available prey (Darnell 1958; Lorio and Shafer 1966; Fontenot and Rogillio 1970; Diener, Inglis and Adams 1974; Danker 1979). This variability in the diet of seatrout makes it difficult to assess the impact of

predation by these fish on shrimp populations and emphasizes the need for information on prey selection by spotted seatrout.

Accurate information on prey selection of predatory fishes cannot be obtained through stomach content analyses without information on the availability of prey species. For planktonic systems, O'Brien and Vinyard (1974) discussed the problems involved in sampling available prey, such as gear selectivity and nonrandom prey distributions in the water column. Determining prey availability may be even more difficult in estuarine predator-prey systems, where predators such as spotted seatrout feed both on the bottom and in the water column. Measurements of prey density do not necessarily measure prey availability to predators. In addition to prey density, availability is affected by differences in prey detectability (Zaret 1972, Kislalioglu and Gibson 1976, Zaret 1980) and catchability (Ivlev 1961, McPhail 1969, Stein 1979), and these two factors can interact with environmental characteristics such as substrate type (Ware 1972, Stein and Magnuson 1976) and the presence of vegetation (Savino and Stein 1982, Minello and Zimmerman 1983). To understand spotted seatrout-shrimp interactions, it is important to know whether seatrout select shrimp over other prey, and whether environmental characteristics, such as the type of substrate, affect selection.

In this study we examined prey selection by spotted seatrout in the laboratory. Prey consisted of juvenile brown shrimp (*Penaeus aztecus*), spot (*Leiostomus xanthurus*), and pinfish (*Lagodon rhomboides*). Equal prey densities and sizes were maintained, and the effect of substrate type on the selection process was determined.

METHODS AND MATERIALS

The six spotted seatrout (160–210 mm TL) used in feeding trials were collected by seine in Galveston Bay, Texas, during the fall of 1982 and spring of 1983. For 1 month prior to observations on prey selection, and between feeding trials, the seatrout were fed equal numbers of live brown shrimp and juvenile spot. Seatrout were examined daily and were only fed after all prey from previous feedings were eaten. This feeding regime gave the seatrout experience with both experimental prey. In addition, the feeding regime was essentially maintained through feeding trials, since an equal number of both prey species was present at the start of each feeding trial. Experience gained in one feeding trial, therefore, should not have strongly affected the results of subsequent feeding trials with the same predators. We considered feeding the seatrout an entirely different type of food before feeding trials, but this procedure can introduce a bias in selection for prey most similar to the type of food chosen (Coppinger 1970).

Prey were collected from Galveston Bay and held in the laboratory for a maximum of 1 week before feeding trials. Shrimp were fed pelleted food, and juvenile fish were fed a commercial flaked fish food or small pieces of shrimp. Juvenile spot were chosen as an alternative prey to shrimp because: 1) spot have been reported to commonly occur in spotted seatrout stomachs (Pearson 1928), 2) juvenile spot are abundant in Galveston Bay throughout the spring and summer, and 3) spot are relatively hardy and survive well in the laboratory.

Observations on selection for brown shrimp versus spot were made in a large elliptical concrete tank (13.4 m^2 bottom area) with an undergravel filtering system and a sand substrate. In the first two feeding trials, which were replicates, a 2-mm plastic mesh was placed over the sand to examine prey selection with no accessible substrate for burrowing. The third and fourth

feeding trials were also replicates and were conducted without the mesh to examine the effect of substrate accessibility. Light was provided through two skylights, and water temperature and salinity were maintained at 26°C and 21–22‰, respectively.

The tank was divided into four sectors of equal size (3.4 m^2 bottom area) by two walls of 3.2-mm plastic mesh. Two spotted seatrout were placed in a release cage (0.6-m diameter) in each of three sectors and starved for 24 hr. Approximately 20 hr before releasing the predators, 20 brown shrimp and 20 spot were measured and placed in each of the four sectors. The fourth sector was used as a control to examine prey interactions and mortality not due to predation by trout. The release cages were lifted at 1200 hr and the trout were allowed to feed for 24 hr. The tank was then drained and the remaining prey in each sector were counted and measured. In the initial feeding trial (one of the two feeding trials with no accessible substrate for burrowing), one of the dividing walls was inadvertently removed after the predators and prey had been introduced, but before the predators were released. In this feeding trial, two of the seatrout were removed, and the four remaining seatrout occupied one half of the tank with 40 shrimp and 40 spot. The other half of the tank was used as the control. Initial densities of both spot and shrimp in all feeding trials were 5.9/m^2.

Similar size-frequency distributions were selected for each prey species to prevent size selection from confounding our results. The size ranges for spot and shrimp were 60–84 mm TL and 59–85 mm TL, respectively. Size-selective predation on shrimp was examined from prey selection feeding trials. Since few spot were eaten when shrimp were present, size-selective predation on spot was examined in an independent feeding trial, in which spot were the only prey available. Again, the initial prey density in each of the three sectors of the experimental tank was 5.9/m^2 (20/sector). The predators were allowed to feed until approximately one-third of the available prey were consumed.

Between feeding trials the spotted seatrout were held in small containers (0.28 to 0.56 m^2 bottom area) with substrates which prevented shrimp from burrowing. Feeding in these holding containers provided an additional opportunity to examine prey selection. One brown shrimp and one spot, of similar size, were offered simultaneously to the seatrout, and the tanks were monitored to determine the prey species eaten first. After the fish had eaten both prey, the process was repeated.

To determine whether spot were avoided as prey in relation to other juvenile fish, prey selection between spot and juvenile pinfish was also examined. For 6 days before observations on selective predation, the seatrout were fed equal numbers of pinfish and spot. One seatrout was then placed in each of six circular cages (0.28-m^2 bottom area) in the large concrete tank. One spot and one pinfish of similar size (58 to 83 mm TL) were added to each cage, and the cages were monitored to determine the prey species eaten first. After 24 hr all remaining prey were removed, and one individual of each prey species was again added to each cage. This procedure was repeated for 6 days.

RESULTS

In the feeding trials conducted in the large concrete tank without an accessible substrate for burrowing, spotted seatrout fed exclusively on juvenile brown shrimp (Table 1). In the two feeding trials with a sand substrate, some spot were eaten, but the seatrout still exhibited a significant selection for shrimp (77 and 78% of the prey eaten were shrimp). Variability among sectors and between replicates of these feeding trials was low (Table 1), which indicated that there was little variability in prey selection among the individual predators and that experience gained during a feeding trial did not affect the results of subsequent feeding trials. A comparison of pooled data from the feeding trials without an accessible substrate and those with a sand substrate showed that the number of each prey species eaten

TABLE 1

Selection by spotted seatrout (160–210 mm TL) for brown shrimp and spot (59–85 mm TL) in 24-hr feeding trials without an accessible substrate for burrowing (without substrate) and with a sand substrate. P = probability that the percentage of shrimp eaten of the total number of prey eaten equals the expected 50% (chi-square analysis).

Feeding Trial	Number of Predators	Number of Prey Present		Number of Prey Eaten		P
		Shrimp	Spot	Total	% Shrimp	
Without Substrate I	4	40	40	19	100	<0.005
Without Substrate II						
Sector 1	2	20	20	9	100	
Sector 2	2	20	20	8	100	
Sector 3	2	20	20	8	100	
Total	6	60	60	25	100	<0.005
Sand Substrate I						
Sector 1	2	20	20	8	75	
Sector 2	2	20	20	6	83	
Sector 3	2	20	20	8	75	
Total	6	60	60	22	77	<0.01
Sand Substrate II						
Sector 1	2	20	20	10	80	
Sector 2	2	20	20	8	75	
Sector 3	2	20	20	9	78	
Total	6	60	60	27	78	<0.005

was dependent upon substrate accessibility ($P < 0.005$, G-test of independence, Sokal and Rohlf 1981). At the initiation of the feeding trials (1200 hr) with sand substrates, 62 and 67% of the shrimp were burrowed (over one-half of the body beneath the substrate surface), and burrowing apparently decreased the availability of brown shrimp to predators.

The control data indicated little interaction between the two prey species. Mortality unrelated to predation was low. Only one of 100 shrimp and four of 100 spot were not recovered alive from the controls over the four feeding trials.

In holding tanks, spotted seatrout also selected brown shrimp over spot as prey. In these tanks, shrimp did not burrow, and only one individual of each prey species was available to the predator. Shrimp were eaten first 81% of the time (21 out of 26 observations), and this percentage was significantly different from the expected 50% (chi-square test, $P < 0.005$).

The feeding behavior of spotted seatrout in the laboratory was similar to the behavior described by Lascara (1981) for weakfish (*Cynoscion regalis*). The seatrout usually approached the prey slowly up to a distance of approximately 10 to 30 cm. If the prey did not swim away during this approach, a rapid strike by the trout generally resulted in prey capture.

Selection between the two prey species in the small holding enclosures did not appear to be related to prey detection since both prey species were approached frequently. The approach of a predator, however, elicited an escape response in spot more frequently than in shrimp. In the larger concrete tank, prey detection was undoubtedly an important factor, especially in the presence of a sand substrate.

When juvenile spot and pinfish were offered as prey, the spotted seatrout fed upon spot first 89% of the time (16 out of 18 observations). This percentage was significantly different from the expected 50% (chi-square test, $P < 0.005$). The relatively short duration of exposure to pinfish as prey (only 6 days versus several months for spot) could have affected these results. Observations on feeding, however, indicated that seatrout often attempted to eat pinfish, but pinfish excaped predatory attacks more frequently than spot.

Shrimp and spot sizes (total length) were similar in all four feeding trials conducted in the concrete tank. Although the seatrout ate shrimp of all sizes, they preferentially preyed upon the small shrimp. Approximately one-half of the initially available shrimp were ≤ 73 mm (Fig. 1), but more than 73% of

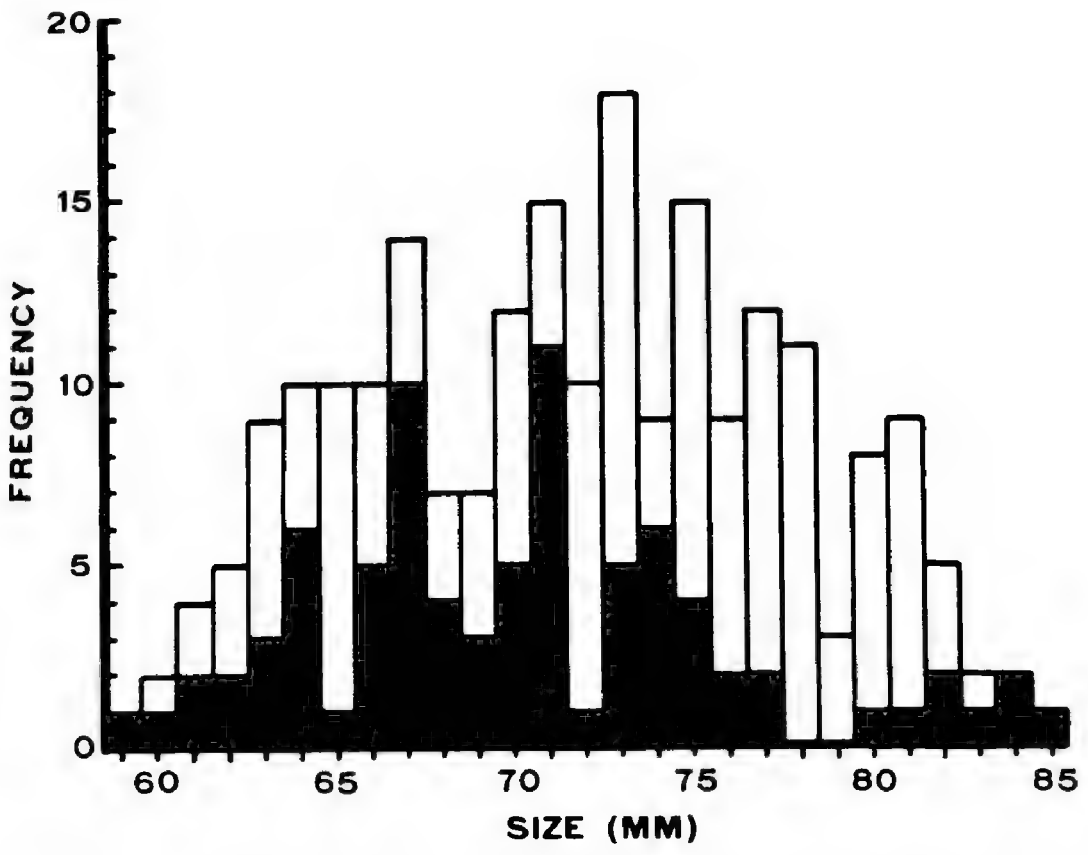

FIG. 1. Size-frequency distributions of brown shrimp eaten (solid bar) and not eaten (open bar) by spotted seatrout (160–210 mm TL) in four selective predation feeding trials. The total height of the bar represents the frequency of each size initially available.

the shrimp eaten were from this half of the size-frequency distribution. The difference between the size-frequency distributions of eaten and not eaten shrimp was highly significant ($P < 0.001$, Kolmogorov-Smirnov two-sample nonparametric test, Sokal and Rohlf 1981). The small number of spot eaten

in the prey selection feeding trials prevented a valid statistical analysis of size selection. In the feeding trials with a sand substrate, however, the 11 spot eaten out of the 120 available were mostly from the lower half of the size-frequency distribution. Seatrout feeding only on spot also selected small prey ($P = 0.006$, Kolmogorov-Smironov test), although the spot available (68–92 mm TL) were slightly larger than in the prey selection feeding trials (Fig. 2).

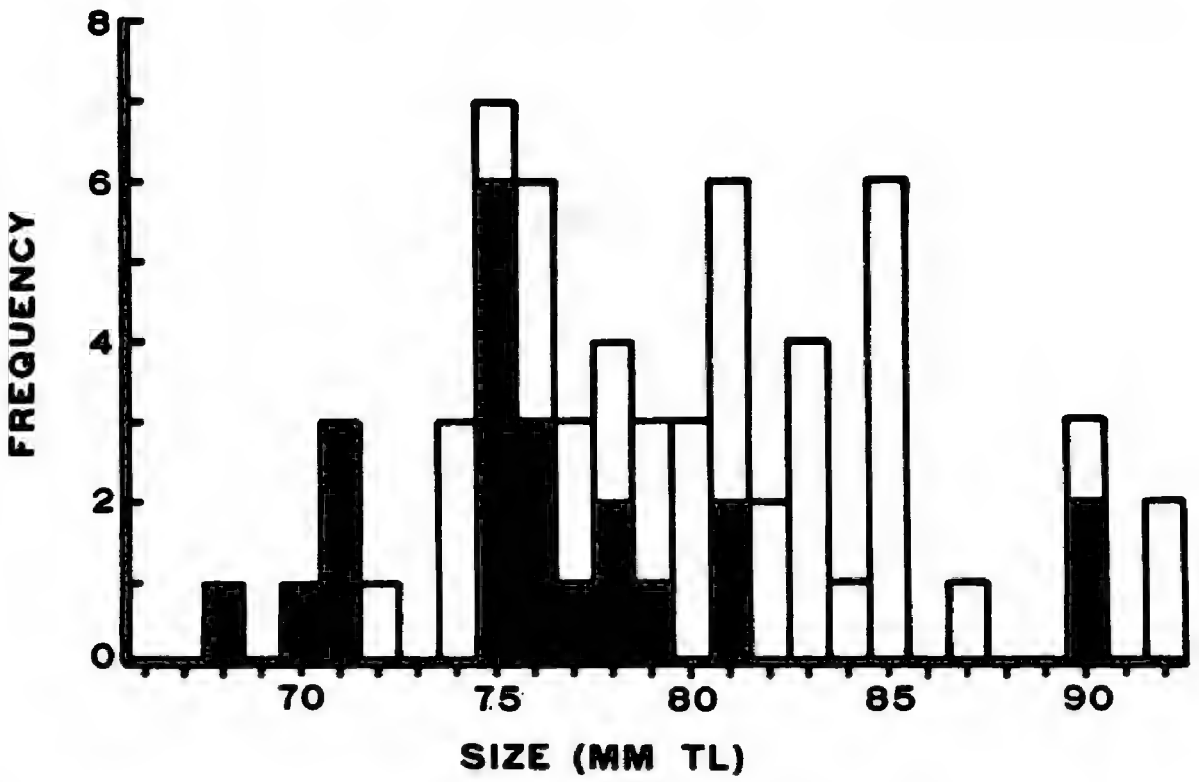

FIG. 2. Size-frequency distributions of spot eaten (solid bar) and not eaten (open bar) by spotted sea trout (170–212 mm TL). Only spot were available as prey, and the total height of the bar represents the frequency of each size initially present.

DISCUSSION

Our laboratory data indicate that spotted seatrout select for brown shrimp over juvenile spot, and for juvenile spot over juvenile pinfish. Both spot (Pearson 1928, Diener *et al.* 1974, Mahood 1974, Danker 1979) and pinfish (Gunter 1945, Moody 1950, Seagle 1969) are natural prey of spotted seatrout, and our results suggest that seatrout select juvenile brown shrimp over juvenile fish as prey.

Behavioral characteristics of prey can reduce their availability to predators, and the presence of prey species in equal numbers does not assure equal availability. Although spotted seatrout fed exclusively on brown shrimp as opposed to spot in experimental tanks without an accessible substrate, burrowing by shrimp in tanks with a sand substrate apparently reduced the availability of brown shrimp and increased predation on spot. Schooling behavior of fish has also been shown to reduce the success of predatory attacks (Neill and Cullen 1974), and schooling by spot may have contributed to our results. In the experimental tanks without an accessible substrate, 20–40 spot were present per sector, and schooling was common.

No spot were eaten in these feeding trials. In holding tanks, prey species were offered in pairs which prevented schooling, and spot were eaten first in 19% of the observations. No burrowing by shrimp occurred in any of these feeding trials. The inability to school may have increased predation on spot in the holding enclosures.

Availability of prey to predators is also dependent upon prey size, which can affect both prey detectability and catchability. A large amount of literature has documented the importance of size-selective predation by fishes in freshwater systems (see Zaret 1980 for review) and estuaries (Parker 1971, Vince, Valiela, Backus, and Teal 1976, Van Dolah 1978, Nelson 1979). Although a narrow range of prey sizes was present in our feeding trials, the spotted seatrout exhibited a significant selection for small prey. This indicates that relatively detailed analyses of the size-frequency composition of potential prey are necessary in field studies, and that the selection of prey species, as determined from stomach content analyses of field-collected spotted seatrout, may in part be related to size-selective predation. Selection by seatrout for small shrimp also has potentially important ecological implications. If predators with the most impact on shrimp mortality, select for small shrimp, shrimp may find refuge from predation in size. Rapid growth rates (0.7–3.3 mm/day) exhibited by juvenile brown shrimp (see Knudsen, Herke, and Mackler 1977 for review) may be an evolutionary response to size-selective predation. A similar hypothesis has been proposed by Parker (1971) for juvenile salmon.

Our study on spotted seatrout confirms the importance of prey availability in selective feeding. The data suggest that under conditions of equal availability, seatrout strongly select brown shrimp over juvenile fish. Behavioral responses of prey to habitat characteristics can alter availability to predators. Burrowing effectively reduces the availability of shrimp, and subsequently their susceptibility to predation. Responses to other habitat characteristics such as vegetation (Zimmerman, Minello and Zamora in press) may function in a similar manner to reduce shrimp availability to fish predators.

ACKNOWLEDGMENTS

We thank the staff of the National Marine Fisheries Service's Southeast Fisheries Center Laboratory in Galveston, and especially E. Martinez, C. Albrecht, S. Dent, and G. Zamora, Jr., for their help in carrying out this study. Assistance with the statistical analyses was provided by Drs. J. Matis and G. Livingston. Suggestions for improving the manuscript were offered by Z. Zein-Eldin, Drs. E. Klima, S. Ray, P. Sheridan, D. Colby, D. Aldrich, and G. Livingston, and by several anonymous reviewers.

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Contributions in Marine Science. (1984) Vol. 27:169–174.

A BREEDING POPULATION OF GULF PIPEFISH (*SYNGNATHUS SCOVELLI*) IN A GEORGIA ESTUARY, WITH DISCUSSION ON THE ECOLOGY OF THE SPECIES

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ABSTRACT

Thirty-four gulf pipefish (*Syngnathus scovelli*) were captured in the Ossabaw Sound/Ogeechee River estuary on the northern portion of the Georgia coastline, 165 km north of the previously described geographical range. Continued capture of gulf pipefish in this estuary over a period of 20 months, the spatial extent of their occurrence, the presence of juveniles, and the presence of males brooding embryos all indicate an established, breeding population. All specimens were collected in intertidal creeks that drain *Spartina* and *Juncus* salt marsh at the fringe of the estuary. The absence of seagrasses, with which this species is closely associated throughout its range, does not exclude the species from inhabiting the salt marsh creek environment. Winter temperatures are colder than in other parts of its range. Water temperatures as low as 5°C and remaining < 10°C from early January through mid-February are within the tolerance range of this species. Dorsal fin ray frequency is substantially greater in the Georgia population than elsewhere in its geographical range. Unusually large males occur in this population, and the sex ratio appears to be heavily skewed toward females.

Accepted 29 February 1984

INTRODUCTION

The gulf pipefish, *Syngnathus scovelli*, previously has been reported to range from Ilha São Sebastão, state of São Paulo, Brazil, northward along the coast of South and Central America, around the coastline of the Gulf of Mexico, and along eastern Florida as far north as the mouth of the St. Johns River (Dawson 1982). This species inhabits shallow (generally < 6 m depth) vegetated waters in coastal and estuarine areas and has been reported from similar habitat in freshwater in Louisiana (Whatley 1962, 1969) and Florida (Gunter 1942, McLane 1955, Hellier 1967). *Syngnathus scovelli* is generally the most abundant pipefish along the coasts of the Gulf of Mexico and eastern Florida (Brown 1972, Dawson 1982).

MATERIALS AND METHODS

Sampling was conducted along the margin of the Ossabaw Sound/Ogeechee River estuary, Georgia (Fig. 1) during investigations on utilization of shallow nursery habitat by fishes. Six

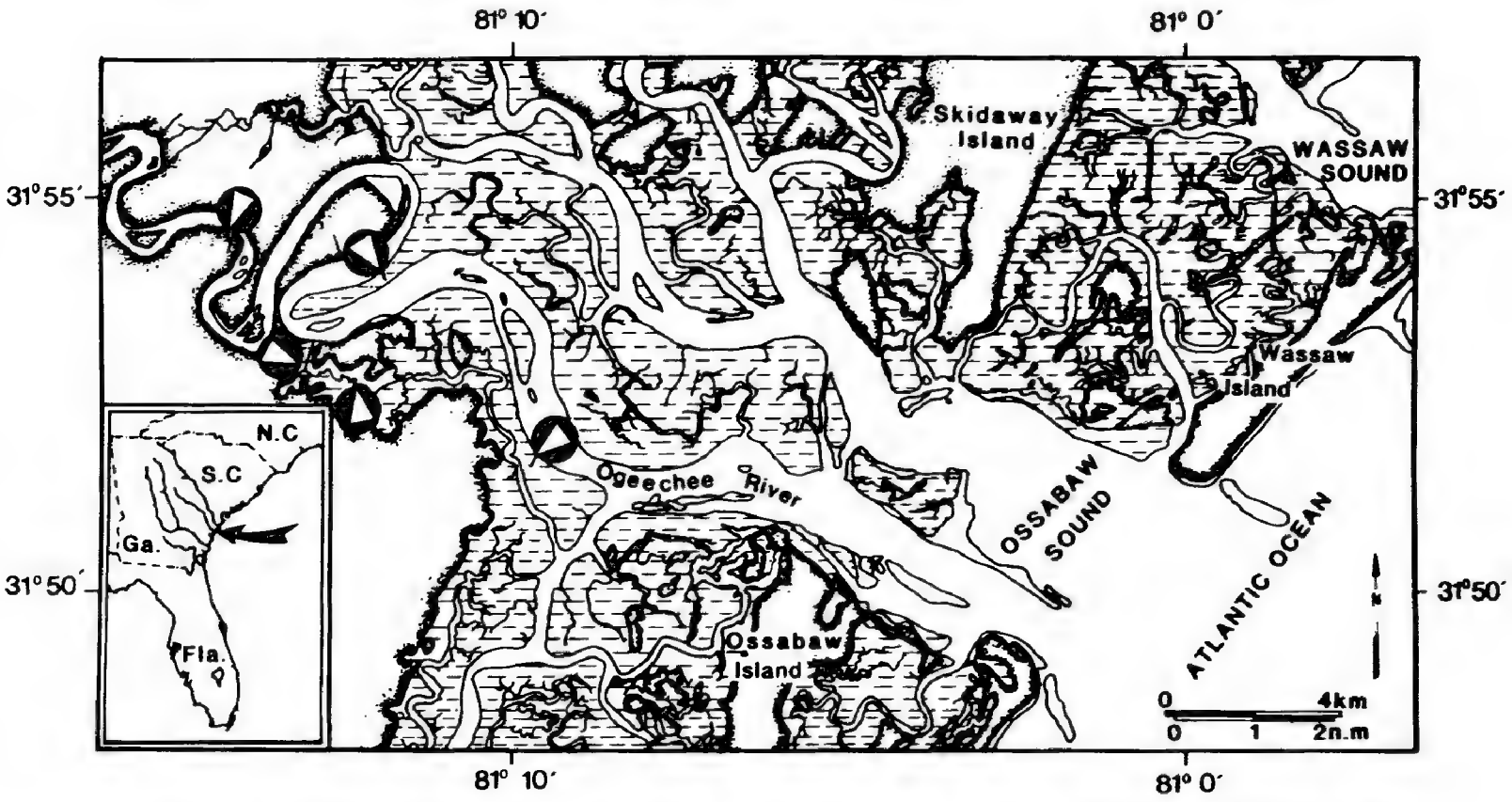

FIG. 1. The Ossabaw Sound/Ogeechee River estuary, Georgia with capture locations of gulf pipefish (*Syngnathus scovelli*). Areas of salt marsh are indicated by horizontal dashed lines.

locations were sampled over several time periods. Sampling frequency varied from more than once per day to once per month, and occasionally occurred irregularly. Fishes were collected by seine in < 2 m of water in intertidal creeks draining smooth cordgrass (*Spartina alterniflora*), rough cordgrass (*Spartina cynosuroides*), and/or needlerush (*Juncus roemerianus*) salt marsh fringing the main body of the estuary. Substrate in these areas ranged from firm sand-clay to very soft mud-detritus.

All *S. scovelli* were measured, and their sex determined by external body features and microscopic examination of gonads. In males, brood size and the arrangement of embryos in the brood pouch was recorded.

RESULTS AND DISCUSSION

OCCURRENCE IN A GEORGIA ESTUARY

Between 9 December 1980 and 20 August 1982, 34 *S. scovelli* were captured at five sampling locations (Fig. 1). Two males, taken on 4 April 1981 and 9 April 1982, carried embryos and developing eggs in their brood pouches. Three pipefish were juveniles. The continued capture of gulf pipefish in this estuary over a period of 20 months, the spatial extent of their occurrence, and the presence of juveniles and males brooding embryos all indicate an established breeding population on the northern portion of the

Georgia coast, 165 km north of the previously described geographical range. This *S. scovelli* population provided information expanding our understanding of the species' ecology.

Although pipefishes are not dominant members of the shallow water fish assemblage in this estuary, *S. scovelli* appears to occur as abundantly as the chain pipefish (*Syngnathus louisianae*). Although northern pipefish (*Syngnathus fuscus*) are known to occur in Georgia estuaries (Dahlberg 1975) none were captured during this sampling.

HABITAT PREFERENCE

Throughout the previously known range, gulf pipefish occur most commonly in brackish and marine bays and inlets where submerged aquatic vegetation occurs over sand or muddy sand bottom. Along the eastern coast of Florida north of Biscayne Bay, gulf pipefish are limited to isolated populations in estuarine areas (such as the Indian River and St. Johns River systems) where seagrass beds occur in brackish waters and other submerged vascular plants occur in freshwater areas behind the open coast beaches. In the St. Johns River, the species occurs primarily in inland freshwater portions of the system. North of the mouth of the St. Johns River, the coast of Florida, Georgia, and much of South Carolina consists of a chain of islands with extensive salt marsh estuaries between and behind the islands. These estuaries have soft sediments and no grass beds. Joseph (1957) speculated that this species' close association with grass beds may determine the northern limit for the species.

It is clear from the presence of *S. scovelli* in salt marsh creeks of the Georgia estuary that soft bottom sediments and the absence of grass beds do not determine the northern limit of distribution. The occurrence of two gulf pipefish in a salt marsh creek near the mouth of the St. Johns River (McLane 1955, Joseph 1957) and their presence in similar habitat along the margin of Apalachee Bay on the Gulf coast of northern Florida (Subrahmanyam and Drake 1975, Subrahmanyam and Coultas 1980) demonstrate that even within their previously reported range, the close association of gulf pipefish with grass beds is not absolute.

TEMPERATURE AND SALINITY RANGE

Gulf pipefish were captured at water temperatures between 13.0 and 30.0°C and salinities from 0 to 22‰. These conditions are within the range reported previously for this species. In the northern portion of the fish's previously described geographical range (approximately 30°N) water temperatures generally do not fall below 10°C (Joseph 1957). Temperatures in the shallow salt marsh creek systems along the northern portion of the Georgia coast can go as low as 5°C, and since the winter of 1979–80 have commonly remained < 10°C from early January until mid-February, with temperatures < 7°C not being unusual (D. Miller unpublished data, T. E. Targett unpublished data). Tolerance of such low temperatures is illustrated

by the fact that these conditions occurred between December and February before the spring and summer capture of eight gulf pipefish, one of which was a male carrying embryos in its brood pouch. These factors establish that temperatures < 10°C over this duration of time are within the tolerance range of this species.

BODY LENGTH AND MERISTICS

The two males captured during the present work were 159 and 153 mm total length (TL) (151 and 146 mm standard length (SL), respectively). The largest male recorded in 717 specimens from 19 localities by Herald and Dawson (1972) was 126 mm SL and in 851 specimens from Tampa Bay, Florida by Springer and Woodburn (1960) was 133 mm SL. It appears that unusually large males occur in this Georgia population. The only reference to male gulf pipefish of comparable size is a maximum of 160 mm TL reported from an isolated freshwater population in Lake St. John, Louisiana (Whatley 1969). Mature male gulf pipefish have previously been found to be smaller than mature females. The length of the largest female captured in the present work (149 mm TL; 142 mm SL) is within the previously reported range.

The numbers of trunk and tail rings and rings covered by the dorsal fin in fish from the Georgia population (Table 1) are similar to those from

TABLE 1

Mean ($\bar{X}$) and range for counts of meristic characters in 34 gulf pipefish (*Syngnathus scovelli*) from the Ossabaw Sound/Ogeechee River estuary, Georgia.

Meristic Character	$\bar{X}$	Range
Trunk rings	16.2	16 - 17
Tail rings	31.9	31 - 33
Total body rings	48.1	47 - 50
Rings covered by dorsal fin:		
Trunk	3.6	3 - 4.5
Tail	4.6	4 - 5.5
Total	8.2	7 - 9.5
Dorsal fin rays	33.5	30 - 36

populations elsewhere (see McLane 1955, Joseph 1957, Brown 1972, Herald and Dawson 1972, Dawson 1982). However, the mean number of dorsal fin rays (33.5) is greater than in 11 of the 12 Florida populations examined by Brown (1972), greater than in 17 of the 19 populations from a large geographical range examined by Joseph (1957), and greater than in all 13 localities from eastern Florida to Brazil examined by Dawson (1982). This high number of dorsal fin rays is also substantially greater than in the St.

Johns River population ($\bar{X}$ = 29) (McLane 1955), the nearest known population. It seems unlikely that there are sufficient isolating mechanisms to result in genetically isolated populations in the virtually continuous system of salt marsh estuaries north of the mouth of the St. Johns River. It is possible that temperatures at which development takes place are sufficiently lower this far north to affect dorsal fin ray numbers, as has been suggested for populations of this species along both coasts of Florida (Brown 1972). It is also possible that not enough fish were captured from the Georgia population to allow an accurate determination of a character that shows such great intrapopulation variation.

SEX RATIOS AND BROOD SIZE

Only two of the 34 individuals captured were males, 29 were females, and the sex of the three smallest immature fish (39, 43, and 45 mm TL) was undeterminable, although microscopic examination indicated they were probably females. This is a male to female ratio of approximately 1:15. Sex ratios previously reported for populations of this species were either balanced (1:1) in the St. Johns River (McLane 1955); varied depending upon time of year between 1:0.7 and 1:2.5 at Cedar Key, Florida and between 1:0.6 and 1:2.4 at Lake Pontchartrain, Louisiana (Joseph 1957); or can be calculated to be 1:1.7 from data on the Tampa Bay population reported by Springer and Woodburn (1960). Therefore, there is evidence that in other *S. scovelli* populations, females are more abundant than males, although not to the extreme indicated in the present data. Joseph (1957) found no evidence for differential spatial distribution of sexes in *S. scovelli* at Cedar Key, Florida, and although the greatly skewed sex ratio in the present work may in part be an artifact of small sample size, it seems that this population is substantially dominated by females.

Females have also been found to outnumber males in populations of other syngnathids. For example, populations of the kelp pipefish (*Syngnathus californiensis*) from the west coast of North America show sex ratios generally varying between 1:3 and 1:8 (Herald 1941), and mature female dusky pipefish (*S. floridae*) outnumber mature males at Cedar Key, Florida (Brown 1972).

The brood pouch of the largest male (159 mm TL) contained 296 embryos and approximately 73 non-developing eggs. This is the largest number of embryos that a male of this species has been found to carry. A maximum of 175 embryos was found in 347 broods from Cedar Key, Florida examined by Brown (1972) and a maximum of 154 was found in over 500 broods from the same location examined by Joseph (1957). The number of embryos carried per cm SL (19.6) is also greater than has been previously reported. The embryos and eggs were arranged in 10 parallel rows, five extending down each side of the major portion of the brood pouch. As the brood pouch narrowed near the posterior end, the number of rows decreased to eight and then to six. Smaller male gulf pipefish usually carry eggs in only two to four

rows, with no more than eight rows previously reported (Brown 1972, Dawson 1982). The large males captured during the present work are able to carry greater numbers of eggs and embryos per unit body length, primarily because a larger diameter brood pouch accommodates more rows.

ACKNOWLEDGMENTS

I thank Messrs. S. G. Rogers, S. B. Van Sant, E. E. Wester, D. M. Wyanski, J. M. Price, T. W. Forbes, and K. S. Crawford for help with the sampling of fish, Dr. D. C. Scott for examining specimens, Mr. D. Miller for providing water temperature data, S. E. McIntosh and A. H. Boyette for preparing the figure, and Drs. D. W. Menzel and N. M. Targett for helpful suggestions on an earlier draft of this manuscript. Support was provided by Skidaway Institute of Oceanography, and the University of Georgia Department of Zoology and Museum of Natural History.

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Contributions in Marine Science. (1984) Vol. 27:175–204

REPRODUCTION AND FOOD HABITS OF SEVEN SPECIES OF NORTHERN GULF OF MEXICO FISHES

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ABSTRACT

Sex ratios, length-weight relationships, maturation, fecundity, and food habits were determined from 7,400 individuals of seven species of inner continental shelf fishes. Samples were taken from trawl catches at depths of 9–91 m between Pensacola Bay, Florida and Brownsville, Texas and from the Campeche Bank, Mexico during the period October 1980–June 1982. Sex ratios favored males in silver seatrout, *Cynoscion nothus*, and Atlantic cutlassfish, *Trichiurus lepturus*, favored females in Atlantic croaker, *Micropogonias undulatus*, hardhead catfish, *Arius felis*, and longspine porgy, *Stenotomus caprinus*, but were equal in sand seatrout, *C. arenarius*, and spot, *Leiostomus xanthurus*. Peak gonadal development was found during spring in longspine porgy, summer in hardhead catfish, spring and late summer in sand and silver seatrouts, spring through fall in Atlantic cutlassfish, and fall in spot and Atlantic croaker. The first Gulf of Mexico fecundity data for six of these species (second record for hardhead catfish) indicated the following maximum fecundities: hardhead catfish—104 eggs; Atlantic cutlassfish—42,100; longspine porgy—43,100; silver seatrout—389,500; sand seatrout—423,100; spot—514,400; and Atlantic croaker—1,075,000. Food habits on either side of the Mississippi Delta were related to age, location, and time of capture. Atlantic cutlassfish were piscivorous. Sand and silver seatrouts preyed on a mixture of fishes and shrimps, and although sand seatrout diets did not vary with age and location, silver seatrout diets did. The remaining species were benthic feeders. Spot fed primarily on polychaetes and detrital matter and secondarily on crustaceans. There were distinct differences in feeding habits of spot between day and night: during the day they ate epifauna, whereas at night they consumed infaunal polychaetes. Atlantic croaker and hardhead catfish diets were dependent upon age: young fish ate polychaetes and older fish preyed upon large, mobile epifauna such as crabs, fishes, shrimps, and stomatopods. Hardhead catfish from the East Delta consumed more polychaetes and less fish and shrimp than did fish from the West Delta. Longspine porgy of all ages consumed mainly polychaetes and detritus both day and night but preyed more upon epifauna in West Delta waters.

Accepted 21 March 1984

INTRODUCTION

Bottomfish stocks in the northern Gulf of Mexico comprise some 200 species, excluding reef fishes, captured out to 100 m depths (Hoese and Moore 1977). Commercial and recreational fisheries yield about 60,000 metric tons/year, while an estimated 300,000 metric tons/year are discarded by commercial shrimp fleets (Gulf of Mexico Fishery Management Council 1980). The highest densities of bottomfishes are found around the Mississippi Delta, and it is there that the fishery is centered. Although a large number of species are caught, seven average 75% by weight of catches on the Delta fishing grounds (Gutherz 1981) and 45–75% off the Texas coast (Chittenden and McEachran 1976). In order of decreasing weight composition, these fishes are Atlantic croaker, *Micropogonias undulatus*; spot, *Leiostomus xanthurus*; longspine porgy, *Stenotomus caprinus*; hardhead catfish, *Arius felis*; sand seatrout, *Cynoscion arenarius*; silver seatrout, *C. nothus*; and Atlantic cutlassfish, *Trichiurus lepturus*. The distributions and abundances of these species have been delimited between Pensacola, Florida and Brownsville, Texas (Roithmayer 1965; Moore, Brusher, and Trent 1970; Gutherz, Russell, Serra, and Rohr 1975; Chittenden and McEachran 1976; Ragan, Melancon, Harris, Falgout, Gann, and Green 1978).

Despite their abundance and commercial importance, research on maturation, reproduction, and feeding of these seven species in offshore waters has been minimal (Gulf of Mexico Fishery Management Council 1980). However, Texas researchers have recently examined the population dynamics and life histories of sand seatrout (Shlossman and Chittenden 1981), silver seatrout (DeVries and Chittenden 1982), and longspine porgy (Geoghegan and Chittenden 1982). In this report, we describe sex ratios, maturation, spawning, fecundity, length-weight relationships, and foods of the seven dominant bottomfishes in the northern Gulf of Mexico.

MATERIALS AND METHODS

Fishes were taken from SEAMAP (Southeast Area Monitoring and Assessment Program) trawl catches made by the NOAA RV *OREGON II*, the Texas Parks and Wildlife Department RV *WESTERN GULF*, and the contract vessel *JEFF AND TINA* primarily between Pensacola Bay, Florida and Brownsville, Texas in 9–91 m waters. Day and night collections were made around the Mississippi Delta (Louisiana to western Florida), and nocturnal collections were made off Texas and the Campeche Bank, Mexico between October 1980 and June 1982 (Table 1). Each vessel towed a 12.2 m semiballoon trawl with tickler chain at 5–6 km/hr. Fishes were collected according to 1) arbitrary depth strate (9–17 m, 18–36 m, 37–55 m, 56–73 m, and 74–91 m), 2) East Delta (87°20′–89°30′ W longitude), West Delta (89°30′–94° W), Texas, or Mexico, and 3) day or night capture. Specimens were preserved in 3.7% formaldehyde-seawater or frozen until analyzed. We present diets only from the East and West Delta areas since foods off the Texas coast have been discussed by Sheridan and Trimm (1983).

Fish were measured to the nearest millimeter standard length (*SL*) except for Atlantic cutlassfish that were measured in total length (*TL*). All were weighed to the nearest 0.1 gram after blotting them dry. Length-weight relationships were determined by regression of log-transformed data. Fishes were presumed to have reached a given age at the following lengths: longspine porgy, Age I = 75 mm, Age II = 125 mm (Geoghegan and Chittenden 1982); spot, Age

TABLE 1

Numbers of bottomfishes collected for reproductive and food analyses by coastal area. Mississippi Delta divided into East (87°20′–89°30′W longitude) and West (89°30′–94°00′W longitude). Mexico collections from 19°30′N latitude, 91°30′W longitude.

	Area				
Species	East Delta	West Delta	Texas	Mexico	Total
Sand seatrout	355	597	233	6	1,191
Silver seatrout	181	474	133	-	788
Spot	309	563	206	-	1,078
Atlantic croaker	376	693	312	15	1,396
Hardhead catfish	138	465	49	7	659
Longspine porgy	532	567	327	-	1,426
Atlantic cutlassfish	320	475	58	-	853
Total	2,211	3,834	1,318	28	7,391
Collection months	11/80, 4/81	10/80,4/81	6/81	3/81	
	10/81, 3/82	6-10/81	7/81		
	6/82	3/82, 6/82	6/82		

I = 125 mm, Age II = 160 mm, Age III = 175 mm (Pearson 1928; Townsend 1956; Sundararaj 1960); Atlantic croaker, Age I = 125 mm, Age II = 200 mm, Age III = 250 mm (Roithmayer 1965; Parker 1971; White and Chittenden 1977; Warren, Perry and Boyes 1978; Gulf of Mexico Fishery Management Council 1980); hardhead catfish, Age I = 150 mm (Lee 1937; Christmas and Waller 1973); sand seatrout, Age I = 150 mm (Shlossman and Chittenden 1981); silver seatrout, Age I = 150 mm (Warren *et al.* 1978; DeVries and Chittenden 1982); Atlantic cutlassfish, Age I = 400 mm, Age II = 700 mm (Dawson 1967). Stomachs were stored in 40% isopropanol. Gonads were examined visually and assigned to one of six maturation stages (undeveloped, immature, developing, maturing, ripe, or spent, after Rohr and Gutherz 1977). All were weighed to the nearest 0.01 g after blotting except undeveloped and spent gonads and testes collected before July 1981. Maturing and ripe ovaries were stored in 40% isopropanol for fecundity estimates. Chi-square analysis was used to detect significant deviations from expected 1:1 sex ratios. A gonadal-somatic index (gonad weight as a percentage of total body weight) was computed for each fish to delimit potential spawning months for each species.

Fecundity was defined as the potential number of eggs that could be spawned over a reproductive season. For fecundity estimates, each pair of ovaries was removed from the preservative, blotted, and weighed to the nearest 0.01 g. Since hardhead catfish ovaries contained relatively few eggs, all yolked eggs were counted. For the other six species, a section was taken from the middle of the paired ovaries, weighed, and placed in water in a gridded petri dish. Eggs in the section were dispersed with forceps and yolked eggs were counted under a dissecting microscope. Section weights ranged between 0.05 and 0.50 g (larger sections contained larger eggs), yielding 400–4,000 eggs per section. Fecundity calculations assumed that eggs developed uniformly throughout the ovaries, all counted eggs would be released, and degeneration or resorption would be negligible. Fecundity was calculated by proportion:

$$\text{Fecundity} = \frac{(\text{eggs in subsample}) \text{ X } (\text{ovary weight}).}{\text{subsample weight}}$$

The relationships of fecundity to fish length, fish weight, and ovary weight were examined by regressions of untransformed and log transformed data, from which we present the best fits.

For each species each month, the stomach contents of all fish in a given age/area/time category were combined for all depths and were washed through sieves to separate similarly sized foods (Carr and Adams 1972). Contents of each sieve were identified microscopically, counted, washed into aluminum pans, and dried at 80–90°C for 24 hr. Dry weights of the foods were calculated from their numerical proportions in each sieve and converted to percentages of total stomach content dry weight. Stomach contents were identified to broad, but exclusive, categories such as sand, polychaetes, shrimps, or fishes. The rarely occurring algae, diatoms, seagrasses, seeds, and woody materials were grouped as plant matter. Fish bones and scales without associated flesh were often found in hardhead catfish stomachs and were given a category. Animal fragments not distinctly referable to any taxon were also categorized. Fine organic matter not referable to any other category was termed detritus. Animal fragments and detritus were tabulated separately from identifiable foods. Shrimps, crabs, and fishes were identified to family or genus, when possible, for qualitative analysis.

RESULTS AND DISCUSSION

MATURATION AND REPRODUCTION

Sand Seatrout

A total of 1,191 sand seatrout was weighed and measured. The relationship between length (*SL*) and weight (*W*) for fish 82–310 mm was:

$$\log_{10} W = 4.46 + 2.86 \log_{10} SL, \text{ where } r^2 = 0.99.$$

Thirty percent (355) of the fish were sexually undeveloped. The overall sex ratio was 436 males to 399 females or 1.09:1, which was not significantly different from a 1:1 ratio ($\chi^2 = 1.55, P > 0.20$). Sex ratios varied monthly but in no consistent pattern. Several investigations of sand seatrout have shown sex ratios favoring one sex over the other. Moffett, McEachron and Key (1979) examined 498 fish from Galveston Bay, Texas and found a male to female ratio of 1:1.66, while Landry and Armstrong (1980) reported a 1:1.32 ratio for 849 fish from western Louisiana. Off Freeport, Texas, however, the sex ratio was 1.30:1 in favor of males among 1,776 individuals (Shlossman and Chittenden 1981). In our samples, sexual identification was first possible for males at 84 mm and females at 82 mm. Smallest maturing fish were 129 and 140 mm for males and females, respectively. Shlossman and Chittenden (1981) found maturing fish at 146 mm and Gunter (1945) recorded a ripe 127-mm male.

Sexually undeveloped fish generally predominated in summer and fall samples (Fig. 1). Maturing and ripe individuals were mainly collected in March and April, although some were collected in August (females) and October (males). Shlossman and Chittenden (1981) postulated spawning from March through September with peaks in March–May and August–September off Freeport, Texas. Landry and Armstrong (1980) collected ripening females in winter off western Louisiana. The monthly variation we observed in gonadal-somatic indices indicated peaks in ovarian development in March–April and in August (Fig. 1) but only a March peak in testicular development, perhaps due to a small number of males sampled.

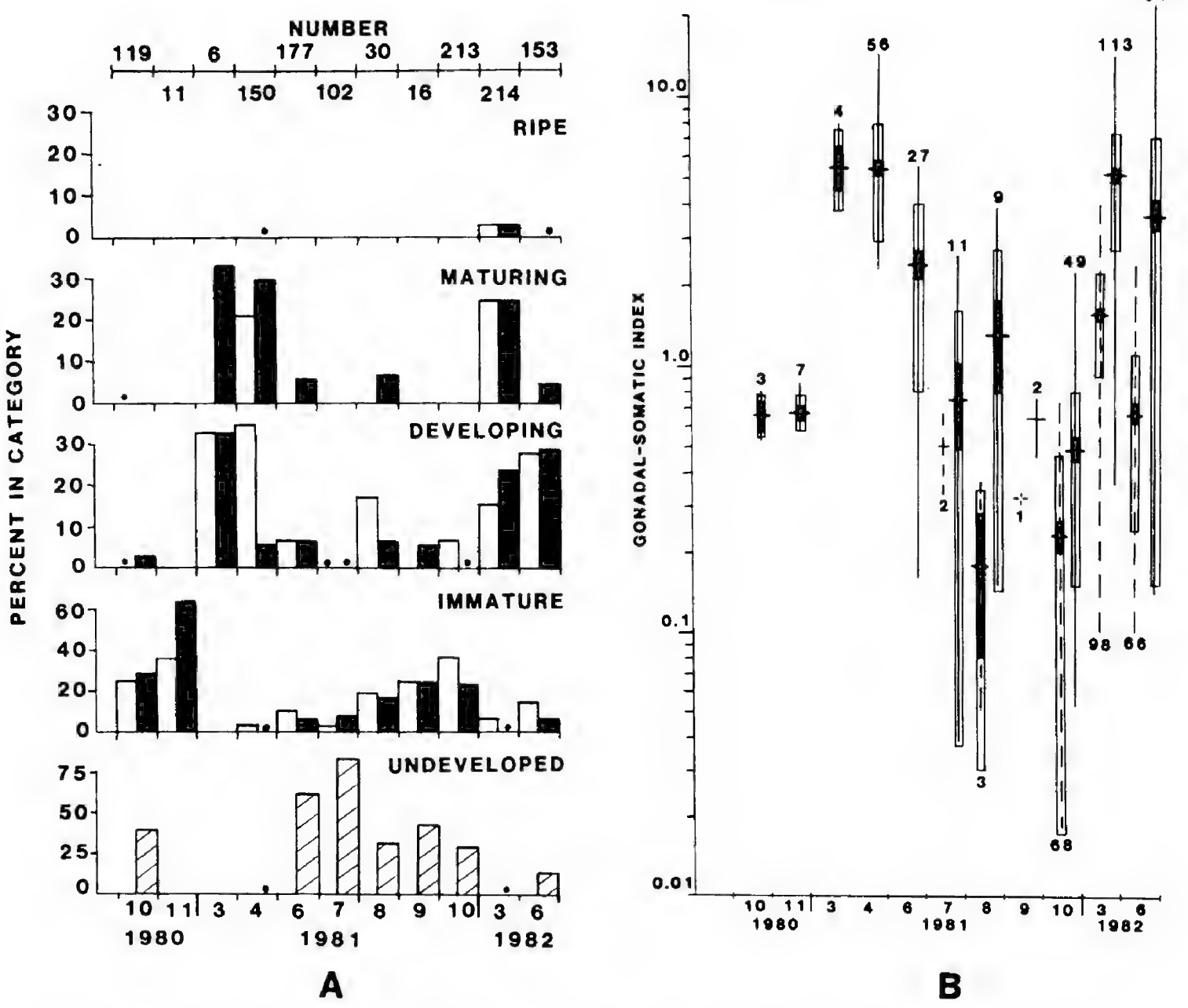

FIG. 1. Sand seatrout. (A) Monthly maturation stages. Open bar = male, black bar = female, shaded bar = undeveloped, dot = ≤ 2% occurrence. (B) Monthly gonadal-somatic indices. Vertical line = range, horizontal line = mean, open rectangle = ± 1 standard deviation, black rectangle = ± 1 standard error. Males indicated by dashed vertical line with number examined below, females by solid vertical line with number examined above.

There is little information concerning sand seatrout spawning habitat. Shlossman and Chittenden (1981) postulated spawning in 7–22 m waters and the lower reaches of estuaries. However, in months when we identified maturing and ripe females, these two sexual stages were relatively more abundant among fish collected from 56–73 m waters (17/45 fish = 38%) than among fish from other depth strata: 9–17 m, 41/294 fish = 14%; 18–36 m, 34/226 fish = 15%; 37–55 m, 32/131 fish = 24%; and 74–91 m, 7/34 fish = 21%. This contrast may be due to different habitats since Shlossman and Chittenden (1981) collected off Texas and our collections during the spawning season centered around the Mississippi Delta.

Fecundity was determined for 131 sand seatrout 140 to 278 mm *SL* (39.1 to 402.5 g). Fecundities ranged from 28,200 for a 210 mm (142.8 g) fish to

423,100 for 247 mm (365.9 g) fish from the Campeche Bank and 324,900 in a 224 mm (223.7 g) fish from the Mississippi Delta region. Fecundity (F) was only moderately related to fish length, fish weight, and ovary weight (OW):

$$F = -198{,}665 + 1{,}480\ SL, \text{ where } r^2 = 0.36;$$
$$F = -\ 8{,}917 + \ 759\ W\ , \text{ where } r^2 = 0.51; \text{ and}$$
$$F = \ 32{,}557 + 7{,}893\ OW, \text{ where } r^2 = 0.53.$$

Our data are apparently the first concerning fecundity of sand seatrout. Merriner (1976) reported that weakfish, *Cynoscion regalis,* from North Carolina have mean fecundities ranging from 44,900 at 145–160 mm to 1,725,900 at 395–480 mm. Sand seatrout are less fecund than weakfish of similar sizes: 140–278 mm sand seatrout averaged 100,900 eggs while 190–268 mm weakfish averaged 285,700 eggs.

Silver Seatrout

Seven hundred eighty-eight silver seatrout, 77–280 mm, were weighed. The relationship between length and weight was:

$$\log_{10} W = -4.63 + 2.94 \log_{10} SL, \text{where } r^2 = 0.98.$$

Sexually undeveloped fish made up 24% (188) of the collection. The overall sex ratio was 328 males to 272 females or 1.21:1, which was significantly different from a 1:1 ratio ($\chi^2 = 5.04, P < 0.05$). Males were more abundant than females in all collections except July–September 1981 when the sex ratio was 1:1.47. Landry and Armstrong (1980) reported a sex ratio of 1:1.72 in spring and summer. We found sexual identification first possible at 77 mm for males and 80 mm for females. Smallest maturing silver seatrout were 140 mm. DeVries and Chittenden (1982) also reported ripe females as small as 140 mm, although Miller (1965) collected 110 mm ripe females.

Sexually undeveloped fish dominated the March–April and October collections (Fig. 2) but also occurred from spring through fall. Ripe females were found only in April and October 1981, but maturing females were collected over a longer period (March–April and August–October). Maturing males were found March through October. This extended maturity season was also reflected in the gonadal-somatic indices (Fig. 2) which showed little monthly variation. Our data suggest that the spawning season begins earlier than May, as proposed by DeVries and Chittenden (1982), and that spawning peaks occur early and late in the season.

Only 18 maturing and ripe female silver seatrout were collected. Their capture at various depths did not indicate a preferred spawning area. Fecundities for these fish, 140 mm (40.1 g) to 256 mm (291.5 g), ranged from 16,800 to 389,500 eggs. Fecundity was strongly related to fish length, fish weight, and ovary weight:

$$F = -362{,}882 + 2{,}570\ SL, \text{ where } r^2 = 0.76;$$
$$F = -\ 52{,}623 + 1{,}309\ W\ , \text{ where } r^2 = 0.84; \text{ and}$$
$$F = \ 32{,}539 + 5{,}662\ OW, \text{ where } r^2 = 0.94.$$

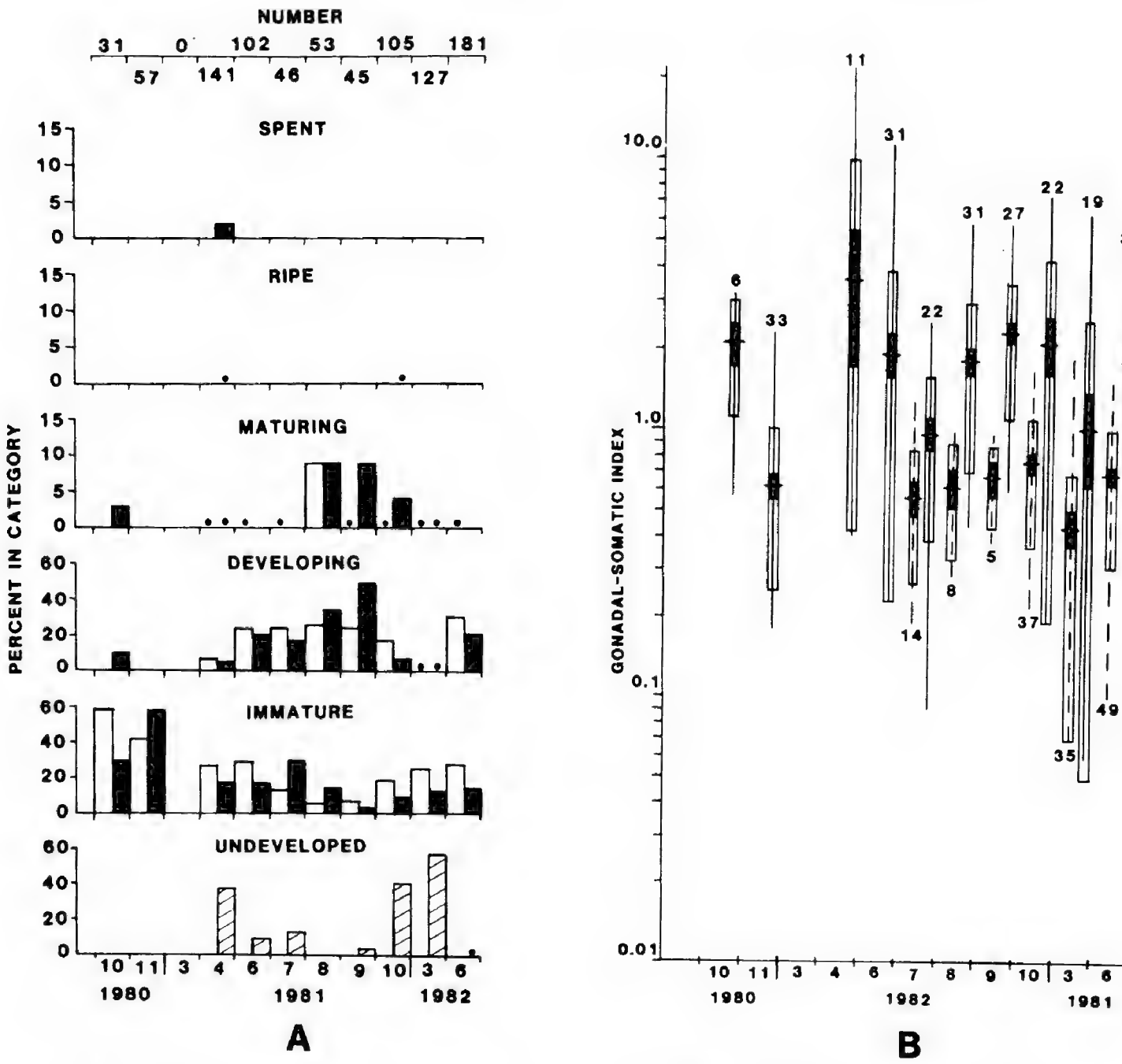

FIG. 2. Silver seatrout. (A) Monthly maturation stages. Open bar= males, black bar = females, shaded bar = undeveloped, dot = ≤ 2% occurrence. (B) Monthly gonadal-somatic indices. Vertical line = range, horizontal line = mean, open rectangle = ± 1 standard deviation, black rectangle = ± 1 standard error. Males indicated by dashed vertical line with number examined below, females by solid vertical line with number examined above.

Our data are apparently the first on fecundity of silver seatrout. Mean fecundity for these individuals was 73,900 eggs, compared to 100,900 eggs in 140–278 mm sand seatrout (this report) and 285,700 eggs in 190–268 mm weakfish (Merriner 1976).

Spot

A total of 1,078 spot, 63–147 mm, was weighed. Length and weight were related by the equation:

$$\log_{10} W = -4.44 + 2.95 \log_{10} SL, \text{ where } r^2 = 0.98.$$

Twenty-eight percent (299) of the fish were sexually undeveloped. The overall sex ratio was 399 males to 380 females or 1.05:1, which was not significantly different from 1:1 ($\chi^2 = 0.42, P > 0.50$). Pristas and Trent (1978) found 1:1 sex ratios in spring and summer but significantly more females during fall and winter in St. Andrew Bay, Florida. Sexual identification was first possible at 70 mm for males and 69 mm for females. Smallest maturing spot were 123 mm males and 127 mm for females. Pearson (1928) collected ripening female spot at 170 mm *TL* (= 130 mm *SL*, Sundararaj 1960).

Sexually undeveloped fish were most abundant in summer collections (Fig. 3). Maturing and ripe spot were collected only in October and November. Although a short fall spawning period is indicated, one ripe male

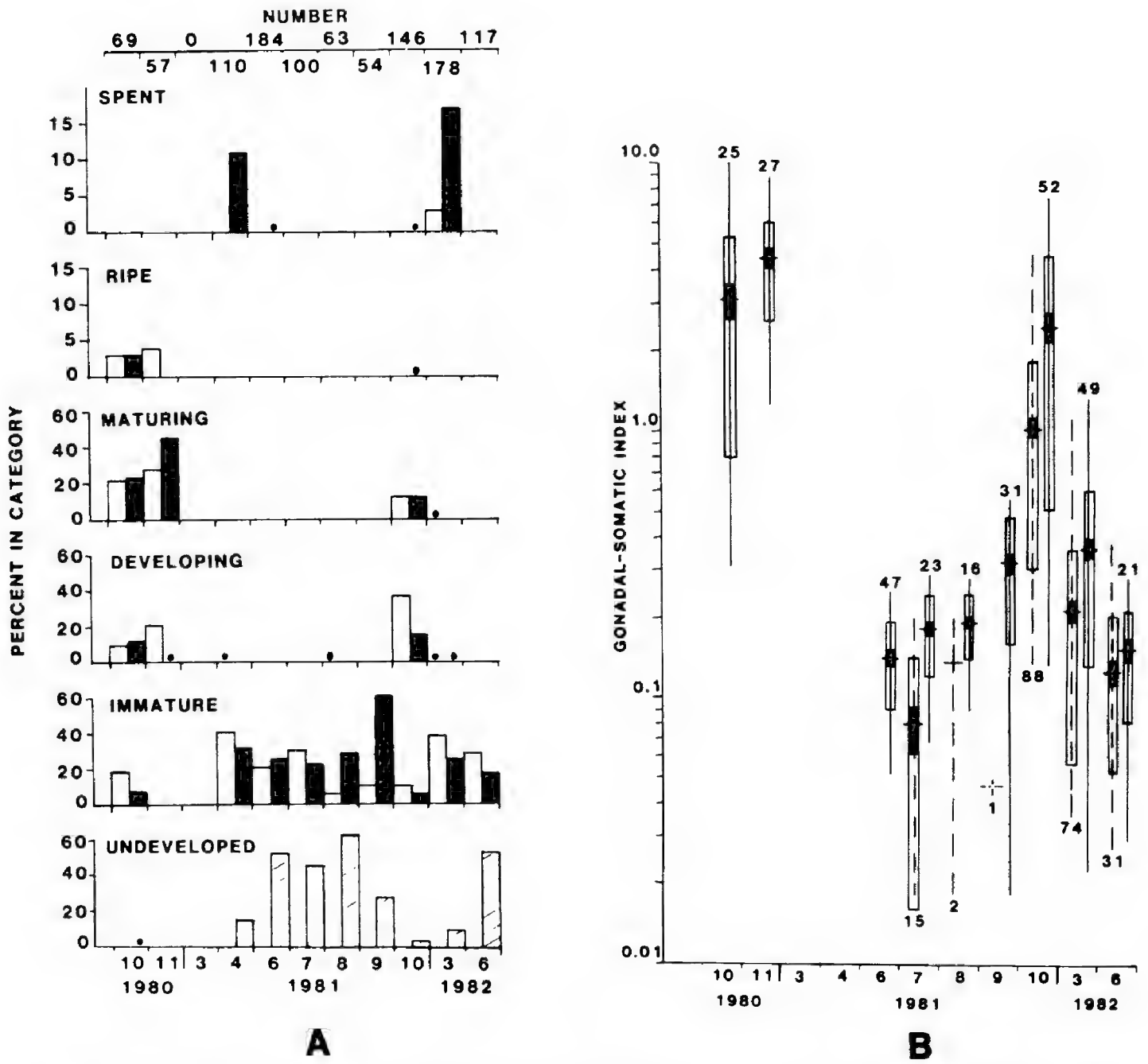

FIG. 3. Spot. (A) Monthly maturation stages. Open bar= male, black bar = female, shaded bar = undeveloped, dot = ≤ 2% occurrence. (B) Monthly gonadal-somatic indices. Vertical line = range, horizontal line = mean, open rectangle = ± 1 standard deviation, black rectangle = ± 1 standard error. Males indicated by dashed vertical line with number examined below, females by solid vertical line with number examined above.

and two maturing females were identified in March 1982 off Louisiana (RV *OREGON II* Cruise 125, B.A. Rohr, NMFS, Pascagoula, Mississippi, personal communication) and we collected a spent female in June 1981. These data suggest a fall through spring spawning season with a fall peak, although we did not collect fish in winter. The monthly variation in the gonadal-somatic indices (Fig. 3) indicated peaks in gonadal development only in the fall. December through February has previously been postulated to be the spot spawning period both off Texas (Pearson 1928) and South Carolina (Dawson 1958). There was no indication that maturing or ripe fish were found more frequently in any one depth stratum.

Fecundity was determined for 64 spot from 127 mm (65.1 g) to 195 mm (208.6 g). Fecundities ranged from 20,900 for a 136 mm (78.3 g) fish to 514,400 for a 178 mm (174.5 g) individual. Fecundity was poorly related to fish length and weight but more strongly related to ovary weight:

$$F = -248{,}965 + 2{,}280\ SL, \text{ where } r^2 = 0.43;$$
$$F = -\ 35{,}589 + 664\ W, \text{ where } r^2 = 0.36; \text{ and}$$
$$F = 9{,}098 + 21{,}244\ OW, \text{ where } r^2 = 0.74.$$

Our data appear to be the second and most extensive report on spot fecundity. Dawson (1958) examined two maturing fish from South Carolina that had fecundities of 77,700 eggs (158 mm *SL*) and 83,900 eggs (187 mm *SL*).

Atlantic Croaker

The relationship between length and weight among 1,396 Atlantic croaker (80–319 mm) was:

$$\log_{10} W = -4.37 + 2.87 \log_{10} SL, \text{ where } r^2 = 0.98.$$

Twenty-three percent (326) of the fish examined were sexually undeveloped. The overall sex ratio was 496 males to 594 females or 1:1.25, which was significantly different from a 1:1 ratio ($\chi^2 = 12.79, P < 0.01$). Males outnumbered females only in the October and November 1980 collections. Landry and Armstrong (1980) found a sex ratio strongly favoring females (1:3.13) in quarterly samples from western Louisiana waters. In our samples, sexual identification was first possible at 84 and 80 mm for males and females, respectively. Smallest maturing fish were 110 mm. White and Chittenden (1977) reported maturation at a similar size (140–170 mm *TL*).

Sexually undeveloped Atlantic croaker were most abundant in the June–August collections (Fig. 4). Maturing fish were noted by September and ripe fish were collected primarily in October and November. Spent females were found in March and April. White and Chittenden (1977) postulated spawning from September to late March but, aside from one spent female identified in June 1982, we found no incidence of spring spawning. Other data from RV *OREGON II* surveys around the Mississippi Delta (Cruise 116, April 1981, and Cruise 125, March 1982, B. A. Rohr, personal communication) indicate no ripe Atlantic croaker among 928 fish examined. Peak gonadal devel-

opment was found in October (Fig. 4). Maturing and ripe fish were collected from 9–73 m depths with no indication of a preferred spawning depth.

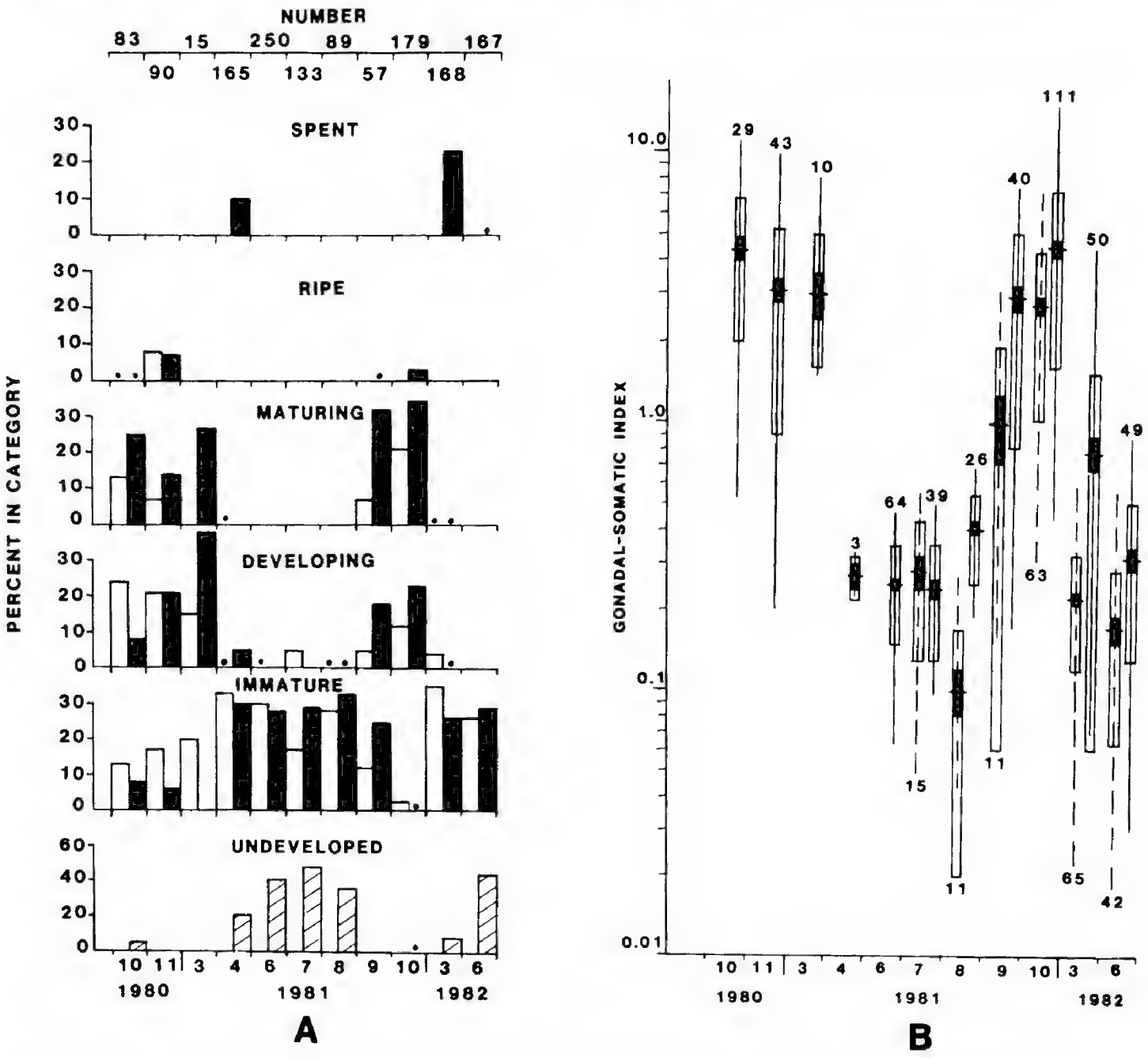

FIG. 4. Atlantic croaker. (A) Monthly maturation stages. Open bar = male, black bar = female, shaded bar = undeveloped, dot = ≤ 2% occurrence. (B) Monthly gonadal-somatic indices. Vertical line = range, horizontal line = mean, open rectangle = ± 1 standard deviation, black rectangle = ± 1 standard error. Males indicated by dashed vertical line with number examined below, females by solid vertical line with number examined above.

Fecundity was determined for 131 fish between 110 and 318 mm (36.7 and 680.4 g). Fecundities ranged between 27,300 for a 132 mm (52.6 g) fish and 1,075,600 for a 318 mm (680.4 g) fish. Fecundity was related to fish length, fish weight, and ovary weight:

$$F = -318{,}340 + 2{,}750\ SL, \text{ where } r^2 = 0.47;$$
$$F = -\ 3{,}248 + 1{,}179\ W, \text{ where } r^2 = 0.63; \text{ and}$$
$$F = 21{,}718 + 17{,}590\ OW, \text{ where } r^2 = 0.81.$$

Morse (1980) examined Atlantic croaker collected between Cape Hatteras, North Carolina and Cape May, New Jersey and reported a fecundity range of

100,800 to 1,742,000 for fish between 196 mm and 390 mm *TL*. No reports on fecundity of Gulf of Mexico fish were located.

Hardhead Catfish

A total of 659 hardhead catfish between 62 and 298 mm was weighed. The majority (540) were collected in 9–17 m waters and only 10 were captured deeper than 37 m. The relationship between length and weight was:

$$\log_{10} W = -4.68 + 2.97 \log_{10} SL, \text{ where } r^2 = 0.99.$$

Of the total examined, 436 or 66% were sexually undeveloped. The overall male to female ratio was 97:126 or 1:1.30, indicating significantly more females than males ($\chi^2 = 4.04$, $P < 0.05$). Only in April and July 1981 were males more numerous than females. The preponderance of females has been recorded elsewhere. Landry and Armstrong (1980) examined 2,236 hardhead catfish from quarterly samples off western Louisiana and found 38% undeveloped fish and a sex ratio of 1:1.98 with females predominating in all sample periods. Ward (1957) reported sex ratios in Mississippi Sound changed from predominantly males in March and April to predominantly females by June, but Pristas and Trent (1978) collected significantly more females during all seasons in St. Andrew Bay, Florida. Etchevers (1978) also found a 1:1.75 male to female ratio for the congeneric *Arius spixii* off Venezuela. The smallest sexually distinct individuals that we found were 141 and 143 mm for males and females, respectively, and the smallest maturing fish were 166 and 180 mm for males and females, respectively. Lee (1937), however, collected gravid females as small as 126 mm and mouth-brooding males at 142 mm in inshore Louisiana waters.

Sexually undeveloped fish dominated all collections except in March 1981 (Campeche Bank, sample of 7 immature fish) and June 1982 (Fig. 5). Although ripe females were collected only in June and July (no ripe males were identified), maturing or spent females were present in 8 of 11 collections. Previous investigators (Lee 1937, Gunter 1947, Ward 1957) have postulated a May–July spawning period in estuarine waters. The monthly variation in the gonadal-somatic indices (Fig. 5) indicated maximum development in June and July. However, results of the visual gonadal classification, coupled with reported collection of 50 mm juveniles in 9–13 m waters off Mobile Bay, Alabama in winter (Gutherz 1981), indicate potential spring through fall spawning with the major peak in early summer.

Fecundity was determined for 27 fish 180 to 298 mm (108.4 to 495.6 g). Fecundities ranged between 6 and 104 eggs (mean = 39). Fecundity was only weakly related to fish length and weight but more strongly related to ovary weight:

$$F = 14.59 + 0.12\ SL, \text{ where } r^2 = 0.14;$$
$$F = 35.67 + 0.02\ W, \text{ where } r^2 = 0.10; \text{ and}$$
$$F = 25.75 + 1.26\ OW, \text{ where } r^2 = 0.68.$$

Ward (1957) found ripe ovaries bearing 40 to 62 eggs 12–14 mm in diameter

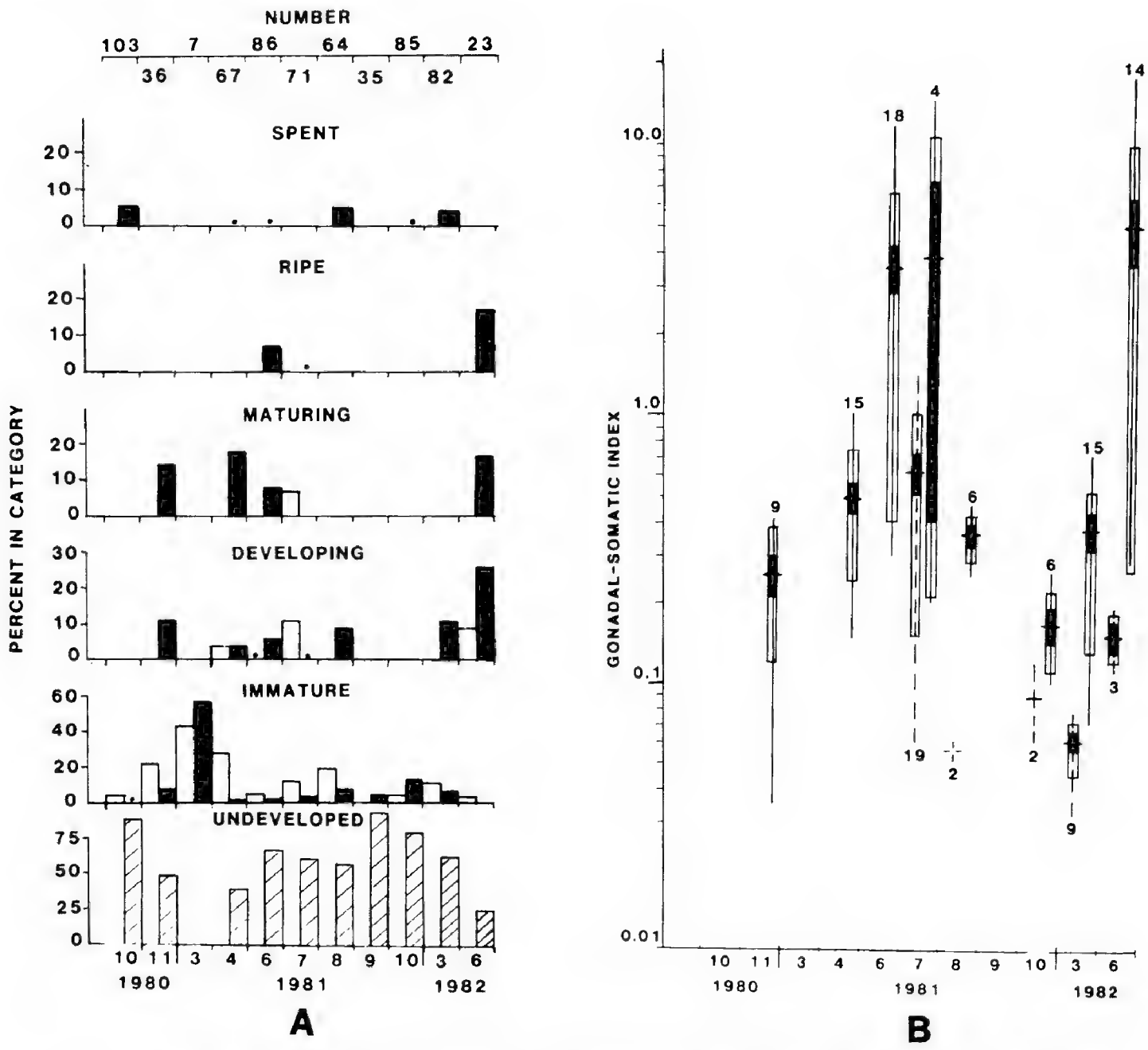

FIG. 5. Hardhead catfish. (A) Monthly maturation stages. Open bar = male, black bar = female, shaded bar = undeveloped, dot = ≤ 2% occurrence. (B) Monthly gonadal-somatic indices. Vertical line = range, horizontal line = mean, open rectangle = ± 1 standard deviation, black rectangle = ± 1 standard error. Males indicated by dashed vertical line with number examined below, females by solid vertical line with number examined above.

with many small, unyolked eggs and stated that ovulated eggs were 14–18 mm wide. We did not collect any males which were mouth-brooding spawned eggs. The largest eggs we measured were 8 mm in diameter. Up to 793 unyolked eggs accompanied the yolked eggs in our samples. The unyolked eggs are apparently released with the viable eggs (Gunter 1947). Fish examined in the present study were in prespawning condition because of small egg diameters, and perhaps because final maturation and spawning occur in estuaries.

Longspine Porgy

The length-weight relationship of 1,426 longspine porgy, 25 to 149 mm, was:

$$\log_{10} W = -4.09 + 2.85 \log_{10} SL, \text{ where } r^2 = 0.97.$$

Sexually undeveloped fish dominated the collections (53.6% or 765 individuals). The overall sex ratio was 293 males to 368 females or 1:1.26, which was significantly different from a 1:1 ratio ($\chi^2 = 8.28, P < 0.05$). Females outnumbered males in all collections except November 1980 and April 1981. Geoghegan and Chittenden (1982) reported a similar sex ratio of 1 male to 1.21 females among 1,506 fish, and Morse (1978) found a 1:1.26 ratio for scup, *S. chrysops*, on the Atlantic coast of the United States. We found that sexual identification was first possible at 60 mm (males) and 52 mm (females). Smallest maturing fish were 77 mm males and 75 mm females.

Sexually undeveloped fish predominated in all but two collections (Fig. 6), representing between 58% and 88% of the fish collected each month. Maturing and ripe fish were found only in April 1981 and March 1982. The monthly gonadal-somatic indices peaked at these times (Fig. 6). Geoghegan and Chittenden (1982) found a similar spawning peak off Texas in February and March in waters deeper than 27 m. During the spawning season, we

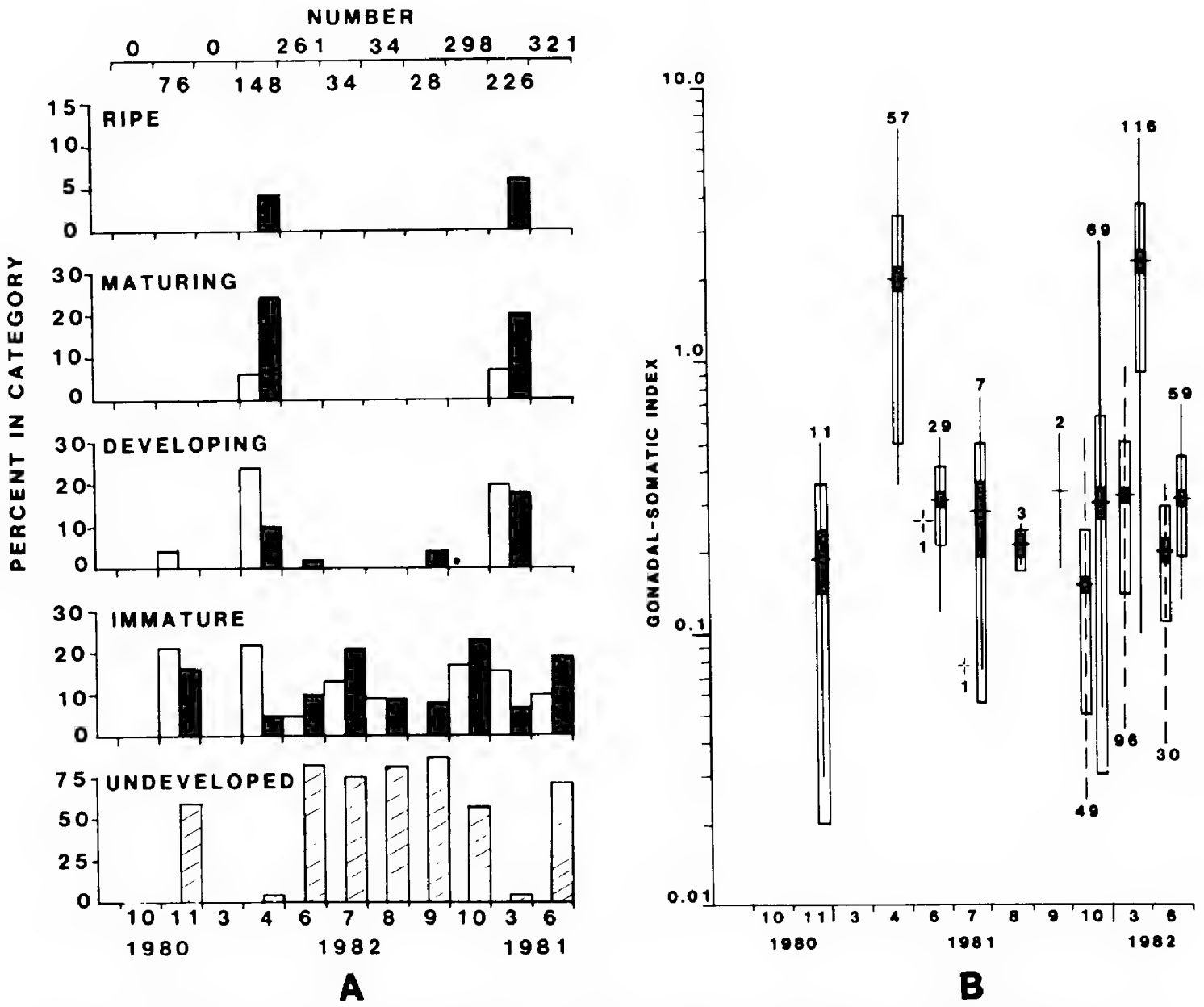

FIG. 6. Longspine porgy. (A) Monthly maturation stages. Open bar= males, black bar = females, shaded bar = undeveloped, dot = ≤ 2% occurrence. (B) Monthly gonadal-somatic indices. Vertical line = range, horizontal line = mean, open rectangle = ± 1 standard deviation, black rectangle = ± 1 standard error. Males indicated by dashed vertical line with number examined below, females by solid vertical line with number examined above.

found maturing and ripe females formed the highest proportions of the population in 56–73 m depths (40/110 fish = 36%) and in 37–55 m depths (35/126 fish = 28%), in contrast to 19% (16/84 fish) in 18–36 m and 20% (8/40 fish) in 74–91 m.

Fecundity was determined for 101 fish 75 to 144 mm (22.9 to 101.4 g). Fecundities ranged between 3,033 in an 82 mm (26.8 g) fish and 43,100 in a 126 mm (71.6 g) individual. Fecundity was poorly related to fish length and weight and moderately related to ovary weight:

$$F = 16{,}262 + 311\ SL, \text{ where } r^2 = 0.28;$$
$$F = 2{,}822 + 271\ W, \text{ where } r^2 = 0.32; \text{ and}$$
$$F = 3{,}307 + 9{,}091\ OW, \text{ where } r^2 = 0.64.$$

Our data are the first concerning the fecundity of longspine porgy. Morse (1978) reviewed biological data on scup, *Stenotomus chrysops*, which are commercially fished between Cape Hatteras and Cape Cod, but found no data on scup fecundity. The red porgy *Pagrus pagrus*, a larger and longer lived sparid, matures at Age II (300 mm TL) and at 600 mm TL could produce 943,000 eggs (Manooch 1976).

Atlantic Cutlassfish

Eight hundred fifty-three Atlantic cutlassfish were weighed and measured, yielding the length-weight relationship:

$$\log_{10} W = -7.28 + 3.37 \log_{10} TL, \text{ where } r^2 = 0.97.$$

Specimens ranged from 133 to 923 mm. Sexually undeveloped fish composed 32% of the collection. The overall sex ratio was 360 males to 220 females or 1.64:1, which was significantly different from a 1:1 ratio ($\chi^2 = 33.31, P < 0.01$). Males outnumbered females in all collections except August 1981. Mericas (1981), however, reported a contrasting 1:1.51 sex ratio in a sample of 250 fish from Mississippi Delta waters. These opposing sex ratios may be due to contrasting sample characteristics: Mericas' specimens ranged between 380 and 1,000 mm *TL* and came only from industrial boats fishing the primary grounds, whereas our specimens came from wider size and geographical ranges. In Cuban waters, Ros Pichs and Castillo (1978) found that sex ratios of 393 Atlantic cutlassfish varied monthly (September–March) but favored males among 500–750 mm fish, females among 800–1050 mm fish, and females overall (280–1050 mm). Chi-square analysis of our data indicated significantly more males than females among 250–499 mm fish ($\chi^2 = 35.01, P < 0.01$) but more females than males in 500–923 mm fish ($\chi^2 = 5.17, P < 0.025$). In our samples sexual identification was first possible at 250 mm (males) or 264 mm (females). Smallest maturing Atlantic cutlassfish were a 387-mm male and a 350-mm female. Comparable identifications among Cuban specimens (Ros Pichs and Castillo 1978) were made with a 500-mm male and a 440-mm female (sexual distinction) and with a 750-mm male and a 710-mm female (first matura-

tion). Different sampling seasons may have caused the wide discrepancy between our results and those from Cuba.

Both sexually undeveloped fish and maturing individuals were found throughout the year (Fig. 7). Ripe females were collected in April, June,

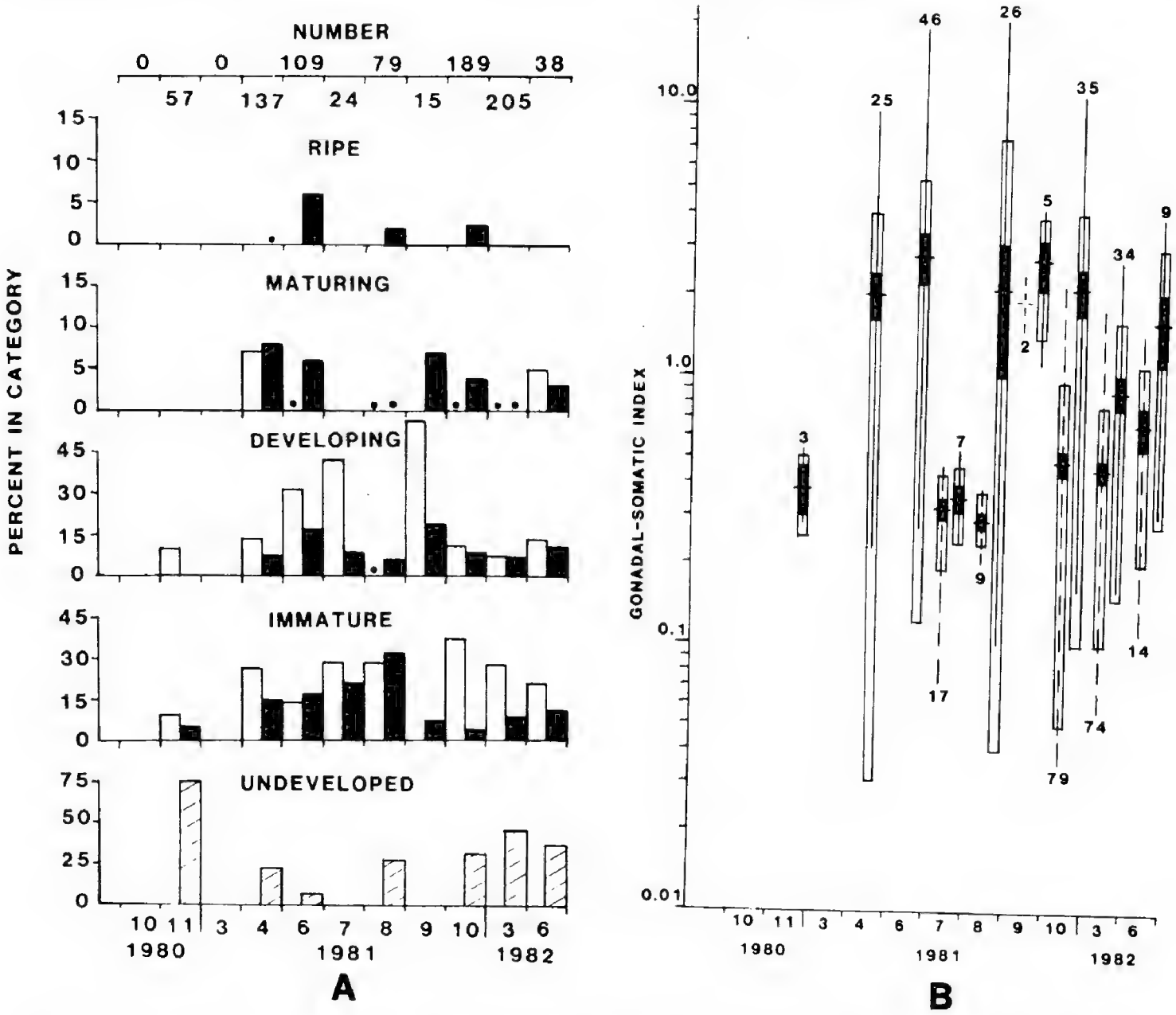

FIG. 7. Atlantic cutlassfish. (A) Monthly maturation stages. Open bar = male, black bar = female, shaded bar = undeveloped, dot = ≤ 2% occurrence. (B) Monthly gonadal-somatic indices. Vertical line = range, horizontal line = mean, open rectangle = ± 1 standard deviation, black rectangle = ± 1 standard error. Males indicated by dashed vertical line with number examined below, females by solid vertical line with number examined above.

August, and October 1981, which indicated an extended spawning season. Monthly gonadal-somatic indices (Fig. 7) also reflected a long season with a possible summer peak. Maturing or ripe fish were collected throughout the 9–91 m depth range sampled. In contrast, Dawson (1967) postulated winter spawning at depths exceeding 36 m (his maximum sampling depth) off Grande Isle, Louisiana. Our widespread sampling, including deeper waters, is the probable source of contrasting results, since similar sampling methods and gear were employed in both our study and Dawson's.

Fecundities were determined for 42 fish 350 mm (30.7 g) to 920 mm (523.2 g). Fecundities varied from 5,000 for a 420-mm (35.9 g) fish to 42,100 for the 920-mm fish but were poorly related to fish length, fish weight, and ovary weight:

$$F = -\ 9{,}705.98 + 47.80\ TL, \text{ where } r^2 = 0.38;$$
$$F = 9{,}026.93 + 64.76\ W, \text{ where } r^2 = 0.41; \text{ and}$$
$$F = 13{,}084.94 + 608.23\ OW, \text{ where } r^2 = 0.13.$$

Our data are the second report on the fecundity of Atlantic cutlassfish. Ros Pichs and Castillo (1978) determined fecundities ranging from 18,000 eggs for a 710-mm (235 g) fish to 193,000 eggs for a 970-mm (735 g) fish. Sources of variation for the lack of correlation between fecundity and ovary weight are discussed later.

FOOD HABITS

Sand Seatrout

We examined 767 sand seatrout stomachs, 471 (61.4%) of which contained food (Table 2). Fishes were the primary food for each age/area/time class

TABLE 2

Stomach contents of sand seatrout, *Cynoscion arenarius*, collected from the Mississippi Delta between October 1980 and July 1982, expressed as percentages of total food dry weight by age, location (East = 87°20′–89°30′W; West = 89°30′–94°00′W), and time of collection. + = < 0.1%.

	Age 0 (33-149 mm SL)				Age I (150-310 mm SL)			
	East		West		East		West	
Stomach contents	Day	Night	Day	Night	Day	Night	Day	Night
Nematodes	-	-	-	-	-	+	+	+
Polychaetes	-	0.7	0.3	-	-	-	-	-
Octopi	-	-	-	-	-	-	-	0.4
Squid	-	-	0.4	-	0.1	10.6	0.9	2.3
Stomatopods	-	-	1.9	-	0.4	3.2	1.8	0.9
Mysids	2.2	-	0.1	-	0.1	+	-	0.1
Isopods	-	-	-	-	-	-	+	-
Amphipods	-	-	+	-	-	-	-	-
Shrimp	36.6	19.6	24.5	2.3	48.4	19.4	28.4	35.1
Crabs	-	0.6	0.6	-	+	0.6	0.5	+
Crab larvae	-	0.9	4.9	-	-	+	+	+
Invertebrate eggs	-	-	-	-	-	-	+	-
Fishes	61.2	78.3	64.3	97.7	51.0	66.2	68.4	61.2
Total identified dry weight (g)	0.663	1.664	3.578	1.998	6.222	34.594	14.057	46.186
Animal fragments (g)	-	0.184	0.110	-	0.351	0.796	0.875	0.524
Detritus (g)	0.040	0.031	0.146	0.007	0.248	0.455	0.831	0.477
Stomachs with food	8	32	105	6	32	83	87	118
Stomachs examined	11	61	129	10	87	140	136	193

(51–98% by dry weight), and shrimps of all types were the second most abundant food (2–48%). On occasion, squid, stomatopods, mysids, or crab larvae comprised up to 11% of the diets. Twelve fish taxa were identified in

sand seatrout stomachs; *Anchoa* comprised 47% and *Bregmaceros* 13%. Other fish taxa occurred only once or twice. Twelve shrimp taxa were noted, most frequently among them *Trachypenaeus* (47%) and *Acetes* (27%). Among other penaeid shrimps, we found six specimens of *Xiphopenaeus*, three *Penaeus*, and two each of *Parapenaeus, Sicyonia*, and *Solenocera.*

Previous investigations in the Gulf of Mexico have yielded results similar to ours. Rogers (1977) reported a diet of 61% (by volume) fish, 20% squid, and 15% shrimp in Age 0 sand seatrout from Texas and Louisiana shelf waters. Off western Louisiana, Landry and Armstrong (1980) found seasonal variations of 51–76% (dry weight) fish and 9–27% shrimp in collections combining Age 0 and I sand seatrout. Sheridan and Trimm (1983) also noted a fish- and shrimp-dominated diet in Texas waters that was little affected by age and habitat.

Silver Seatrout

A total of 632 silver seatrout stomachs were examined, of which 429 (67.8%) contained food (Table 3). Fishes were the primary food of 7 of 8

TABLE 3

Stomach contents of silver seatrout, *Cynoscion nothus*, collected from the Mississippi Delta between October 1980 and July 1982, expressed as percentages of total food dry weight by age, location (East = 87°20′–89°30′W; West = 89°30′–94°00′W), and time of collection. + = < 0.1%.

	Age 0 (32–149 mm SL)				Age I (150–280 mm SL)			
	East		West		East		West	
Stomach contents	Day	Night	Day	Night	Day	Night	Day	Night
Nematodes	-	-	0.2	-	+	-	0.3	+
Polychaetes	-	-	+	0.4	-	-	-	-
Gastropods	-	-	0.2	-	-	-	-	-
Bivalves	-	-	0.8	-	-	-	-	-
Squid	-	-	-	8.9	-	1.2	+	2.8
Calanoid copepods	0.2	5.3	-	+	-	-	-	+
Stomatopods	0.1	-	0.8	0.4	-	2.5	0.4	0.4
Mysids	19.2	14.1	0.5	1.5	-	-	+	1.7
Cumaceans	0.2	0.1	0.1	0.1	-	-	+	-
Amphipods	0.6	0.7	0.1	0.8	-	-	0.2	0.7
Shrimp	46.8	11.2	26.8	32.2	0.4	24.1	14.8	42.1
Shrimp larvae	-	-	-	+	-	-	-	-
Crabs	0.2	-	1.8	0.8	1.6	1.5	1.2	0.6
Crab larvae	1.6	-	0.3	-	0.1	-	1.1	0.9
Insects	0.2	-	-	-	-	-	-	-
Fishes	30.2	65.6	65.7	55.0	97.9	70.8	81.9	50.8
Total identified dry weight (g)	0.442	1.494	3.404	2.288	2.937	8.893	4.681	4.771
Animal fragments (g)	0.012	0.070	0.549	0.117	0.033	0.098	0.466	0.247
Detritus (g)	0.018	0.048	0.789	0.162	0.042	0.176	0.371	0.438
Stomachs with food	21	55	134	71	7	29	57	55
Stomachs examined	30	68	188	90	27	38	105	86

age/area/time classes (51–98% by dry weight), the exception being Age 0/East/Day where shrimps were the main prey (47%). Shrimps were

generally the second most abundant food, comprising 0.4–47% of the diet. Mysids were important food (14–19%) to Age 0 fish on the East Delta but not on the West Delta. Squid, calanoid copepods, stomatopods, and crab larvae occasionally formed between 1% and 9% of the diet. Age 0 and East Delta fish generally ate more shrimp and less fish than did Age I and West Delta fish. Nine fish taxa and 8 shrimp taxa were found in silver seatrout stomachs. *Bregmaceros* (30%), *Anchoa* (30%), and *Centropristis* (10%) were the most frequently identified fish genera; 6 other taxa occurred only once. *Acetes* (35%), *Trachypenaeus* (31%), and alpheids (17%) were the most common shrimps. One specimen of each of the penaeids *Sicyonia* and *Solenocera* were identified.

Fish and shrimp have been reported elsewhere as the primary foods of silver seatrout in the Gulf of Mexico, but previous studies have generally involved smaller individuals and have not considered age or time of capture as possible factors influencing diets. Rogers (1977) collected 26–175 mm specimens from western Florida into Texas waters and found an overall diet of 56% fish and 19% shrimp by volume. He documented a shift from a 40% shrimp–18% mysid diet in 26–50 mm fish to a 77% fish–8% shrimp diet in 76–175 mm fish but did not specify collecting times. Landry and Armstrong (1980) reported a seasonal shift in diet off western Louisiana from fish in spring and summer to shrimp in fall. Their nocturnal collections consisted mainly of Age 0 fish from a single location. In collections limited to nocturnal samples over a short summer period, Sheridan and Trimm (1983) found that age and depth of capture influenced diets off Texas.

Spot

We examined 760 stomachs and found only a small proportion (32.7%) containing food (Table 4). Spot have relatively small stomachs that are easily ruptured when expanded by food. Swim bladder expansion after trawl capture in many cases burst the stomachs and intestines, rendering the specimen useless for food analysis. Although 140 Age II and III specimens were collected, they usually came from deeper water and empty or ruptured stomachs were prevalent. Data from these fish were minimal and were thus included with the Age I data. Spot consumed a wide variety of foods, but polychaetes and detrital matter formed the bulk of the diet. Calanoid copepods and amphipods were prominent daytime foods on both sides of the Mississippi Delta, as were cumaceans on the east side, while polychaete consumption was generally higher at night in both areas. *Acetes* and *Lucifer* were the only shrimps found, and we were unable to identify any of the rarely occurring crabs or fishes.

Two other studies of the offshore foods of spot have been conducted. Chen (1976) collected spot primarily from the East Delta region in fall and winter. Her largely Age I–III individuals had consumed detritus/sediment (68% by volume), polychaetes (23%), shrimp (6%), and amphipods (2%). Our data from the same area indicated similar consumption of polychaetes, shrimp, and amphipods but lower intake of detritus (17–22%) and higher intake of

TABLE 4

Stomach contents of spot, *Leiostomus xanthurus*, collected from the Mississippi Delta between October 1980 and July 1982, expressed as percentages of total food dry weight by age, location (East = 87°20′–89°30′W; West = 89°30′–94°00′W), and time of collection. + = < 0.1%.

	Age 0 (63-124 mm SL)			Age I (125-197 mm SL)			
	East		West[a]	East		West	
Stomach contents	Day	Night	Day	Day	Night	Day	Night
Sand	-	4.5	1.6	4.5	22.3	4.4	-
Plant matter	-	-	0.2	-	1.5	0.1	0.1
Nematodes	-	1.8	1.4	2.6	3.2	0.1	-
Polychaetes	11.4	94.1	71.6	23.9	34.3	63.0	92.6
Gastropods	-	-	0.1	-	-	0.2	-
Bivalves	-	0.6	0.4	0.7	2.2	0.6	-
Ostracods	-	-	+	-	-	-	-
Calanoid copepods	12.3	-	11.4	17.2	0.9	11.8	0.4
Harpacticoid copepods	-	0.3	2.6	0.8	0.6	0.2	0.2
Stomatopods	-	-	-	-	-	0.2	-
Mysids	-	-	2.3	1.2	0.6	2.1	-
Cumaceans	49.5	0.3	0.2	28.1	2.7	0.3	-
Isopods	-	-	0.1	0.2	+	+	-
Amphipods	8.1	0.2	3.6	11.5	2.7	5.3	0.1
Shrimp	0.6	0.3	2.8	6.8	+	7.1	2.0
Shrimp larvae	-	-	-	-	0.5	0.1	-
Crabs	-	-	0.1	0.8	0.1	2.8	1.2
Crab larvae	-	-	0.4	-	-	0.2	0.2
Insects	-	-	-	-	0.8	-	-
Ophiuroids	16.5	-	-	0.2	0.1	-	-
Sea urchins	-	-	-	-	0.2	-	-
Sand dollars	-	-	-	-	+	-	-
Lancelets	-	-	-	-	26.9	+	-
Fishes	-	-	1.2	-	0.2	1.5	3.2
Fish eggs	1.6	-	-	1.5	0.1	-	-
Total identified dry weight (g)	0.043	0.348	0.338	0.193	1.429	1.134	0.391
Animal fragments (g)	0.003	0.104	0.226	0.020	0.351	0.165	0.069
Detritus (g)	0.046	0.070	0.377	0.044	0.495	0.435	0.024
Stomachs with food	3	10	75	30	55	54	22
Stomachs examined	9	27	143	82	174	173	152

[a] No Age 0 spot were collected from the West at night

calanoid copepods, cumaceans and lancelets. Off the Texas coast (Sheridan and Trimm 1983), Age 0 spot fed mainly upon detritus (62%) and various crustaceans while Age I spot consumed less detritus (37%) and began preying upon fish (17%).

Atlantic Croaker

The stomachs of 430 of 976 fish (44.1%) contained food (Table 5). Only 2 of 11 Age III fish stomachs contained food, and data from these fish were combined with that from Age II. Our data indicate that while Age 0 Atlantic croaker tended to feed upon polychaetes (67–79% of their diets), Ages I and II fish fed upon larger, mobile organisms such as stomatopods (59% by Age II/East/Day and Night), shrimps (28–100%), crabs (59% by Age I/East/Night, 68% by Age II/West/Day), or fishes (5–40%). Atlantic croaker preyed

TABLE 5

Stomach contents of Atlantic croaker, *Micropogonias undulatus*, collected from the Mississippi Delta Between October 1980 and July 1982, expressed as percentages of total food dry weight by age, location (East = 87°20′–89°30′W; West = 89°30′–94°00′W), and time of collection. + = < 0.1%.

	Age 0 (80-124 mm SL)			Age I (125-199 mm SL)				Age II (200-318 mm SL)			
	East[a]	West		East		West		East		West	
Stomach contents	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
Sand	-	-	+	-	7.1	-	-	-	0.7	-	-
Plant matter	-	-	-	+	-	-	-	-	-	-	-
Nematodes	-	0.4	0.8	1.0	0.4	0.2	0.1	0.2	-	-	-
Polychaetes	67.1	79.0	76.3	24.2	14.3	69.3	18.1	5.8	2.7	-	-
Gastropods	-	-	-	-	+	-	-	-	-	-	-
Bivalves	-	0.1	-	+	-	-	-	-	-	-	-
Squid	-	0.5	-	-	0.8	-	-	-	-	-	-
Calanoid copepods	-	-	+	+	-	0.1	0.1	-	-	-	-
Barnacles	-	-	+	-	-	-	-	-	-	-	-
Stomatopods	-	-	-	15.6	-	2.1	3.2	58.6	58.9	10.4	-
Mysids	-	0.1	0.3	0.9	+	0.2	0.1	-	-	-	-
Isopods	-	-	-	-	-	-	-	+	-	-	-
Amphipods	-	0.1	0.1	0.3	0.1	+	+	-	0.1	-	-
Shrimps	13.8	10.9	7.4	28.2	7.2	4.9	32.2	0.3	32.1	-	100.0
Crabs	7.8	1.3	11.0	10.3	59.2	9.3	6.2	-	0.2	68.1	-
Crab larvae	-	0.1	-	+	-	0.1	-	-	-	-	-
Invertebrate eggs	-	0.1	-	0.5	0.3	0.1	-	0.3	-	-	-
Tunicates	-	+	-	-	-	-	-	-	-	-	-
Lancelets	-	-	-	-	+	-	-	-	-	-	-
Fishes	11.0	5.3	4.0	18.9	10.1	13.6	40.0	34.7	5.4	21.4	-
Fish eggs	-	+	-	-	0.4	-	-	-	-	-	-
Total identified dry weight (g)	0.090	1.737	1.198	1.229	2.759	2.341	3.040	1.196	3.185	1.053	1.528
Animal fragments (g)	-	0.632	0.120	0.137	0.521	0.344	0.687	0.545	0.082	-	0.013
Detritus (g)	0.027	0.815	0.073	0.305	0.520	0.533	0.545	0.105	0.096	-	0.017
Stomachs with food	8	130	48	29	57	75	62	9	8	2	2
Stomachs examined	16	160	59	102	201	174	209	22	24	6	3

[a] No Age 0 fish were collected from the East during daylight

upon seven taxa of shrimps (primarily *Acetes* (33%) and *Trachypenaeus* (19%) of those identified), five crab taxa (one occurrence each of *Albunea*, *Callinectes*, pagurids, *Raninoides*, and xanthids), and four types of fishes (50% *Bregmaceros*).

The feeding habits of Atlantic croaker have been the subject of numerous studies in the Gulf of Mexico, most of which have shown that polychaetes are the primary food of smaller individuals and large crustaceans and fishes are added to the diet with growth (Chen 1976, Rogers 1977, Overstreet and Heard 1978, Landry and Armstrong 1980, Sheridan and Trimm 1983). These same reports show the variability in diet components; for example, Chen (1976) observed similar diets among size classes, but Sheridan and Trimm (1983) found no correlations in diets among Age 0 and I in two habitat types.

Hardhead Catfish

Almost all of the 547 stomachs contained food (92.7%). Fish ranged up to 298 mm *SL* and probably included some Age II individuals, but little is known of the growth rates and longevity of the species. Hardhead catfish ingested a broad spectrum of foods (Table 6). Feeding habits were affected

by both age and area but not by time of day. Age 0 fish from the East Delta preyed mainly upon polychaetes (64% and 68% of the diets), but consumed fewer polychaetes and more shrimp and fish bones and scales on the West Delta. Small sample sizes from the East Delta may have been responsible for these differences. Age I hardhead catfish also consumed some polychaetes (8–33% of the diets) but began preying upon larger epifauna such as stomatopods, shrimps, and fishes on the West Delta and crabs on the East Delta. Hardhead catfish preyed upon 10 shrimp taxa, dominated by burrowing alpheids and *Ogyrides* (29%), epifaunal *Trachypenaeus* (23%), and planktonic sergestids such as *Acetes* and *Lucifer* (17%). Among 14 taxa of crabs, we found *Pinnixa* most often (29%), followed by xanthids (22%),

TABLE 6

Stomach contents of hardhead catfish, *Arius felis*, collected from the Mississippi Delta between October 1980 and July 1982, expressed as percentages of total food dry weight by age, location (East = 87°20′–89°30′W; West = 89°30′–94°00′W), and time of collection. + = < 0.1%.

	Age 0 (62-149 mm SL)				Age I (150-298 mm SL)			
	East		West		East		West	
Stomach contents	Day	Night	Day	Night	Day	Night	Day	Night
Sand	0.3	0.2	0.2	-	1.3	3.9	0.2	-
Plant matter	-	-	+	-	-	0.8	+	-
Anemones	-	-	0.5	-	-	-	-	1.0
Rhynchocoels	-	-	0.9	-	-	-	-	-
Nematodes	-	0.4	+	-	+	+	+	+
Polychaetes	68.0	64.4	40.1	18.7	32.6	9.8	23.5	7.6
Gastropods	-	-	0.2	0.2	3.5	0.1	0.2	0.1
Bivalves	-	-	-	-	+	0.4	0.2	-
Squid	-	-	+	-	-	0.2	+	-
Calanoid copepods	6.9	0.2	0.5	+	+	+	+	-
Harpacticoid copepods	-	0.5	+	-	+	-	-	-
Barnacles	-	-	-	-	0.1	-	-	-
Stomatopods	0.1	-	1.8	-	0.4	13.9	16.2	16.3
Mysids	0.1	4.8	+	2.9	+	0.2	+	+
Cumaceans	1.6	0.8	+	-	-	+	-	-
Isopods	-	-	-	-	-	-	-	0.2
Amphipods	1.2	4.0	0.3	-	0.1	0.5	-	-
Shrimps	0.3	3.0	7.1	17.9	1.5	3.2	19.2	47.6
Shrimp larvae	1.4	0.9	0.1	-	+	+	+	+
Crabs	9.5	3.7	10.2	3.1	36.4	37.3	18.6	10.8
Crab larvae	0.6	0.8	1.0	0.4	0.1	0.1	+	+
Invertebrate eggs	1.1	-	1.9	-	0.3	+	0.3	+
Insects	-	-	0.6	-	-	0.1	+	-
Holothurians	-	-	0.3	-	-	-	1.4	-
Chaetognaths	-	-	-	-	+	-	-	-
Lancelets	0.1	2.7	-	-	-	0.1	-	-
Fishes	3.0	-	0.3	2.5	3.1	1.1	6.2	10.9
Fish bones + scales	4.8	0.4	33.8	39.6	13.6	28.2	13.9	5.3
Fish eggs	1.1	13.4	+	14.7	0.1	0.1	+	-
Total identified dry weight (g)	0.549	0.673	4.736	1.806	10.663	19.224	36.822	28.165
Animal fragments (g)	0.147	0.130	1.957	1.o81	1.557	5.341	6.760	2.783
Detritus (g)	0.093	0.057	1.193	0.882	0.905	3.632	2.654	0.494
Stomachs with food	5	9	159	32	35	79	133	55
Stomachs examined	5	9	165	32	36	88	148	64

pagurids (12%), and *Ovalipes* (10%). Fifty percent of the 7 taxa of prey fishes were *Anchoa.*

Only two other quantitative studies have examined the offshore foods of hardhead catfish. Landry and Armstrong (1980) reported crabs and polychaetes as the primary spring through fall foods of Age I fish in the Weeks Island, Louisiana area. Sheridan and Trimm (1983) found that during summer nights off Texas, hardhead catfish prey primarily upon stomatopods, crabs, shrimps, and holothurians.

Longspine Porgy

Slightly more than half of the longspine porgy stomachs examined contained food (595/1,096, 54.3%). A wide variety of food was consumed but two main feeding groups emerged: East Delta versus West Delta (Table 7). Longspine porgy from the West Delta generally consumed more shrimps, crabs, and fishes and less polychaetes than did fish from the East Delta. Some age-related changes in diet were apparent, as older individuals tended to consume more fish and fewer polychaetes. Because longspine porgy tend to macerate food, prey taxa were rarely identified. Alpheids appeared to be the most frequent shrimp, while *Raninoides* and xanthids were the only crabs identified.

Henwood, Johnson and Heard (1978) examined longspine porgy diets from the East Delta region and noted that polychaetes, amphipods, crabs, shrimps, and harpacticoid copepods were the most frequently occurring foods. Unfortunately, their data were only summaries even though day and night collections and Ages 0–II were sampled. Rogers (1977) found polychaetes to be the primary food in West Delta and Texas waters and that Age I individuals consumed more fishes and shrimps than did Age 0 fish. Sheridan and Trimm (1983) also found polychaetes to be the primary food of fish off Texas.

Atlantic Cutlassfish

We examined 743 Atlantic cutlassfish stomachs and 560 (75.4%) contained food. This species was almost exclusively piscivorous (Table 8), but occasionally consumed large amounts of squid and shrimps. Although 12 taxa of fishes and 4 taxa of shrimps were identified, 50% of the fishes were *Anchoa* and 76% of the shrimps were *Acetes.* Mericas (1981) and Sheridan and Trimm (1983) reported that Atlantic cutlassfish were piscivores.

SUMMARY AND CONCLUSIONS

REPRODUCTION

Some of our result agree and others contrast with those of previous studies of reproduction in these Gulf fishes. Sex ratios for Atlantic croaker, hardhead

TABLE 7

Stomach contents of longspine porgy, *Stenotomus caprinus*, collected from the Mississippi Delta between October 1980 and July 1982, expressed as percentages of total food dry weight by age, location (East = 87°20′–89°30′W; W = 89°30′–94°00′W), and time of collection. + = < 0.1%.

	Age 0 (25-74 mm SL)				Age I (75-124 mm SL)				Age II (125-149 mm SL)		
	East		West		East		West		East		West[a]
Stomach contents	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day
Sand	9.2	18.4	6.8	-	4.8	0.5	3.5	2.9	11.6	-	-
Plant matter	-	-	-	-	-	0.2	-	-	-	-	-
Rhynchocoels	5.5	-	-	-	-	-	-	-	-	-	-
Nematodes	1.1	-	-	-	0.2	0.3	0.8	1.8	-	-	-
Polychaetes	68.4	56.9	41.8	42.7	68.8	82.4	61.2	45.9	19.7	22.5	22.9
Gastropods	-	-	6.8	-	0.1	-	+	-	-	72.2	-
Bivalves	-	-	-	-	5.5	0.1	-	1.3	1.9	-	-
Squid	-	-	-	-	1.7	-	-	11.7	-	-	-
Ostracods	-	-	-	-	-	-	-	0.3	-	-	-
Calanoid copepods	1.1	0.3	4.7	3.0	0.3	0.1	0.7	0.4	1.5	-	-
Harpacticoid copepods	-	-	1.6	-	+	0.1	-	-	-	-	-
Barnacles	-	-	-	-	-	-	-	-	-	-	19.3
Stomatopods	9.4	-	-	-	0.4	+	1.0	2.0	10.6	-	-
Mysids	-	3.6	-	36.0	0.1	4.7	0.1	0.2	-	-	-
Cumaceans	-	-	-	-	0.1	+	-	-	1.0	-	-
Isopods	-	-	-	-	-	-	+	-	-	-	-
Amphipods	-	2.1	5.7	-	0.7	1.7	0.5	1.9	-	-	-
Shrimps	-	7.8	26.1	12.8	8.2	4.0	12.5	5.1	2.5	-	17.6
Crabs	-	5.4	6.8	-	2.1	3.4	9.0	11.3	21.2	-	3.2
Crab larvae	-	3.1	-	-	-	0.5	0.3	+	-	-	-
Invertebrate eggs	-	-	-	-	-	0.1	3.4	-	0.6	-	0.1
Brachiopods	4.7	0.4	-	-	0.7	0.1	-	-	-	5.3	-
Fishes	1.1	1.4	-	5.2	6.1	1.3	6.9	15.2	29.6	-	37.1
Fish eggs	-	-	-	-	0.2	-	-	-	-	-	-
Total identified dry weight (g)	0.036	0.078	0.019	0.152	1.264	1.517	1.112	0.982	0.150	0.016	0.697
Animal fragments (g)	0.035	0.040	0.015	0.102	0.516	1.034	0.251	0.464	0.121	0.038	0.008
Detritus (g)	0.011	0.130	0.013	0.075	0.580	0.256	0.357	0.629	-	0.011	0.056
Stomachs with food	7	43	12	40	107	147	89	117	14	6	13
Stomachs examined	10	56	19	79	162	250	166	281	28	15	30

[a] No Age II fish were collected from the West at night

TABLE 8

Stomach contents of Atlantic cutlassfish, *Trichiurus lepturus*, collected from the Mississippi Delta between October 1980 and July 1982, expressed as percentages of total food dry weight by age, location (East = 87°20′–89°30′W; West = 89°30°–94°00′W), and time of collection, + = < 0.1%. Age II data summed due to small numbers collected.

	Age 0 (133-399 mm TL)				Age I (400-699 mm TL)				Age II (700-923 mm TL)
	East		West		East		West		East + West
Stomach contents	Day	Night	Day	Night	Day	Night	Day	Night	Day + Night
Squid	-	-	+	-	-	0.1	24.2	32.7	-
Calanoid copepods	0.2	5.5	+	-	-	-	-	-	-
Stomatopods	0.1	0.2	+	0.5	-	-	-	-	-
Mysids	0.4	0.3	-	-	-	-	-	-	-
Amphipods	0.2	-	+	-	-	-	+	-	-
Shrimp	4.7	8.8	16.5	8.3	2.7	1.6	16.1	1o.3	5.1
Crabs	-	-	-	-	-	-	+	-	-
Crab larvae	0.9	0.1	0.2	0.2	+	-	0.5	-	-
Fishes	93.5	85.0	83.2	91.0	97.3	98.3	59.0	56.9	94.9
Total identified dry weight (g)	4.652	2.271	16.969	4.213	7.064	10.556	6.691	2.778	23.802
Animal fragments (g)	0.509	0.019	0.163	0.052	0.203	0.007	0.550	0.004	0.010
Detritus (g)	0.076	0.046	0.029	0.033	0.186	0.014	0.108	0.006	0.069
Stomachs with food	134	29	235	33	44	12	48	17	8
Stomachs examined	187	35	284	48	58	13	70	37	11

catfish, and longspine porgy have been found to favor females, while sex ratios for spot, Atlantic cutlassfish, and sand and silver seatrouts vary from study to study. We feel that our data are representative of northern Gulf populations because of our extensive collections. For six of the seven species, our data on reproductive cycles compare favorably to data from previous studies. We disagree only with Dawson (1967), who proposed winter spawning for Atlantic cutlassfish. Our data indicate relatively high reproductive activity from April through September. Our gonadal-somatic indices represent the first such quantitative information for Gulf fishes. Ovarian development appears to be continuous during the spawning seasons of all seven species as indicated by a mixture of egg sizes in maturing and ripe ovaries. The fishes probably release eggs several times during the spawning period. Goldberg (1976, 1981) has described similar spawning in three California sciaenids, *Genyonemus lineatus*, *Seriphus politus*, and *Cheilotrema saturnus*, which are morphologically similar to Atlantic croaker, seatrout, and spot, respectively (Miller and Lea 1972).

Longspine porgy, Atlantic croaker, and spot apparently have high reproductive activities in spring or fall. However, lack of sampling from December through February could have led us to describe incompletely their reproductive cycles. Geoghegan and Chittenden (1982) examined ovarian development of longspine porgy from October 1978 through March 1980 in Texas waters. They recorded peak frequencies of gravid females in March 1979 and again in March 1980. Winter probably represents a ripening period around the Mississippi Delta as well, since our data indicate March and April as spawning months. We observed a peak gonadal-somatic index for female Atlantic croaker in October 1980, followed by a decline in November 1980, a subsequent rise in August–September 1981, and another peak in October, 1981. This sequence appears to define the major reproductive peak for the species around the Mississippi Delta, while winter represents the final stages of reproduction. We apparently did not characterize the peak gonadal development of spot, based upon Pearson's (1928) conclusion of maximum spawning activity in January and February off Texas.

Our fecundity data are, for the most part, new information for Gulf of Mexico fishes. Few comparisons could be made for these species or their congeners along the Atlantic coast. Within the Gulf, silver seatrout appear less fecund than sand seatrout. Both seatrouts are less fecund than the Atlantic coast weakfish, and Atlantic croaker appear less fecund in the Gulf of Mexico than in the Middle Atlantic Bight at similar sizes. Longspine porgy are much less fecund than Atlantic coast red porgy due to their small size. Atlantic cutlassfish from the Gulf appear less fecund than those from Cuba.

Length, weight, and ovary weight are traditionally explored as predictors of fish fecundity (Bagenal 1967), and one or more of these factors usually explains much of the variation in fecundity estimates. For our data, ovary weight was the most reliable predictor of fecundity except in Atlantic cutlassfish. However, poor to moderate predictive capacities were found in most of our fecundity regressions. Potential sources of variation include: 1)

ovaries which appeared ripe but were actually in prespawning condition or which had already released some or all of the ripe eggs, thus inflating the egg counts by including a greater number of small diameter eggs per unit weight of ovary; 2) ovaries collected across an extended spawning period (with one or more peaks in spawning activity) which would be influenced by seasonal changes in metabolic activity, and which would cause inaccurate counts on either side of peak gonadal development; or 3) violation of our assumptions of uniform egg development and no degeneration or resorption of eggs. An extended spawning period is characteristic of batch or repeat spawners (Nikolskii 1969) and, among the fishes we examined, only longspine porgy apparently have a short (1–2 month) spawning season. The queenfish, *Seriphus politus*, is a batch-spawning sciaenid which exhibits a 3–6 month spawning period (longer for larger females) that is characterized by a single peak in gonadal indices, a weekly spawning frequency, and a decline in egg size as the spawning season progresses (DeMartini and Fountain 1981). Such factors could have affected our regression analyses since ovaries used for fecundity estimation were collected in 4–6 months of the spawning seasons of each of our species except spot and longspine porgy. We note that other investigators have reported ovary weight as an excellent predictor of fecundity (r^2 = 0.89–0.98) in fishes such as Atlantic menhaden, *Brevoortia tyrannus* (Dietrich 1979), Atlantic croaker (Morse 1980), and yellow flounder, *Limanda ferruginea* (Howell and Kesler 1977), all of which have 3–6 month spawning periods. However, fecundity estimates in these studies were based on ovaries collected only during probable peak spawning over periods of 40, 12, and 2 days, respectively. Our sampling strategy may thus be partially responsible for the variation in fecundity. Finally, we do not know whether or not ovaries of our species exhibit uniform development, or degeneration or resorption of eggs, traits which apparently vary among species. For example, uniform egg development throughout the ovary is found in vermilion snapper, *Rhomboplites aurorubens* (Grimes and Huntsman 1980) but not in bluefin tuna, *Thunnus thynnus* (Baglin 1982). Degeneration and resorption of eggs have been seen in weakfish (Merriner 1976) but not in queenfish (DeMartini and Fountain 1981).

The more abundant fishes on the Gulf of Mexico continental shelf have been characterized by Chittenden and McEachran (1976) as small, short-lived species with high annual mortality rates. We have noted here that the seven dominant species also reproduce at or before Age I. Although they appear to have common life history strategies, there are differences in reproductive patterns relating to season, duration of spawning, and fecundity.

FOOD HABITS

Diets were analyzed by age, area, and time of day. Neither sand seatrout nor Atlantic cutlassfish, both piscivores, altered their diets in response to these factors. Only the spot diet appeared to be affected by time of capture

(age and area had little effect), since polychaete consumption was higher at night and predation on small crustaceans was higher during the day. Age influenced the Atlantic croaker diet as fish moved from infaunal to large epifaunal prey with growth, and area had a similar effect on the feeding of longspine porgy. Age and area influenced the diets of silver seatrout and hardhead catfish. Older silver seatrout, particularly from the East Delta, ate more fishes and less shrimps than did younger, West Delta fish. Like Atlantic croaker, older hardhead catfish consumed more large epifauna and less infauna than did younger individuals. Polychaetes and crabs were more abundant in East Delta hardhead catfish stomachs than in West Delta stomachs, while the reverse was generally noted for stomatopods, shrimps, and fishes. The change in diet with age of the benthic feeding Atlantic croaker and hardhead catfish is likely related to the increase in mouth size which enables older (larger) fish to prey upon larger epifaunal organisms. Predation upon larger organisms was also seen in spot, but to a much lesser extent. The influence of area upon diets probably reflects differences in available prey on either side of the Mississippi Delta. To our knowledge, a comparative analysis of the abundance and composition of the benthic faunas of the East and West Delta continental shelves has not been made.

Given the diversity of potential prey organisms around the Mississippi Delta, it is important to note that only a few taxa regularly occurred in the diets. Among prey fishes, *Anchoa* and *Bregmaceros* were most frequently observed in stomachs of both epibenthic and benthic feeders. *Anchoa* spp. are abundant in estuaries (Christmas and Waller 1973) but are less often captured offshore (Chittenden and McEachran 1976; Ragan *et al.* 1978). *Bregmaceros* is common in the northern Gulf of Mexico but it is rarely caught except in plankton nets due to its small size and nocturnal migrations off the bottom (Dawson 1966). Perhaps some behavioral component or an underestimated abundance makes these two taxa such important prey. Only Atlantic croaker and hardhead catfish consumed crabs to any extent. Fourteen crab taxa were identified, and *Pinnixa*, xanthids, and pagurids were found most often. Xanthids and pagurids are common shallow water crabs (Bedinger 1981), but *Pinnixa* spp. have not been reported as such. Both benthic and epibenthic feeding fishes seemed to prefer the shrimps *Acetes* and *Trachypenaeus*. *Acetes* is a small, common planktonic shrimp (Franks, Christmas, Siler, Combs, Waller, and Burns 1972; Bedinger 1981) apparently easily preyed upon by various sizes of fish. Penaeid shrimps were often eaten, particularly by seatrouts, as representatives of six genera were identified. *Trachypenaeus* spp. are common on the continental shelf (Franks *et al.* 1972; Bedinger 1981) but usually less numerically abundant than commercial *Penaeus* spp. Yet here and elsewhere (Rogers 1977, Divita *et al.* 1983, Sheridan and Trimm 1983), it is reported that fish prey more often upon *Trachypenaeus* than upon *Penaeus*. One likely reason for this phenomenon is that *Trachypenaeus* is a much smaller shrimp than offshore *Penaeus* spp. In summer trawl catches off the Texas coast, Divita *et al.* (1983) found the average *Trachypenaeus* weighed 4–6 g and the average *Penaeus*

aztecus weighed 10–37 g, while the associated fish fauna averaged 19–50 g. Concurrently, *Trachypenaeus* was found in 4.10% of the 7,374 fish stomachs examined while only 0.18% of the fish consumed *Penaeus*.

ACKNOWLEDGMENTS

We thank Lorrie Sullivan for laboratory assistance, Frank Patella and Dennis Koi for computer programming, Estella Garcia and Deomeria Ackerman for data entry, Jane Doherty and Beatrice Richardson for typing various drafts, Daniel Patlan for graphics, and numerous reviewers for constructive criticism.

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DISTRIBUTION AND COMPOSITION OF LARVAL FISH POPULATIONS WITHIN ALAZAN BAY, TEXAS

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ABSTRACT

Ichthyoplankton samples taken in Alazan Bay, Texas, from September 1978 through November 1979 yielded 6571 larval and postlarval specimens of at least 13 species. *Gobiosoma* sp. and *Anchoa mitchilli* comprised > 91% of the total catch and were the only species present in every season. Larval fish abundance peaked in May; however, catch rates were statistically consistent during the Fall 78, Spring 79, Summer 79, and Fall 79, while the Winter 78 seasonal catch rate was significantly lower. Larval fish abundance was correlated with photoperiod, temperature, and salinity.

Accepted 19 April 1984

INTRODUCTION

Information concerning the larvae of estuarine-dependent marine fishes and their environmental needs is limited. This paucity of information can be partially attributed to the complex life cycles of marine fishes which require several different habitats including the use of estuaries as nurseries (Pearson 1929; Gunter 1945; Miles 1950, 1951; Chapman 1966; McHugh 1966). Population stability of these species is dependent upon the survival of the larvae within the estuary. Houde (1973), Gjøsaeter and Saetre (1974), and Tanaka (1974) suggested that egg and larval fish concentrations could be used as an indicator of future year class strengths and stock recruitments. However, the theoretical aspects and practicality of this premise was questioned by Hunter (1976) partially on the basis of the lack of information concerning the early life history of most marine fishes. Considering that a large portion of the sport and commercial harvest of finfish on the Texas coast is comprised of estuarine-dependent species (TPWD 1975a, 1975b), the need for a complete understanding of the ecology of ichthyoplankton within the estuaries is essential.

There have been no previous studies of larval fishes in Alazan Bay or adjacent bays. Farther to the north, King (1971) examined the movement of larval fish into and out of Mesquite Bay through Cedar Bayou. Pearson (1929), Miles (1950, 1951), and Simmons and Breuer (1962) conducted life history studies of some sciaenids in the waters of Aransas Bay and other surrounding bays. These studies dealt with spawning times and sites as well as the estuarine dependence of the larvae. The presence and movement of larval fishes in the Aransas and Corpus Christi Channels were investigated by Bradley and Compton (1963) and in the Aransas, Port Mansfield, and Brazos Santiago Channels by Compton (1965). Ichthyoplankton in Nueces Bay was sampled by Henley and Rauschuber (1979) as part of an investigation into the freshwater needs of that estuary.

Hoese (1965) used data on larval and juvenile concentrations in the Gulf waters near the Aransas Pass Channel to identify spawning times and locations of fishes and subsequent migrations by some species through the channel into the estuaries. Larval fish distribution over the continental shelf along the southern coast of Texas was examined by Angelovic (1976) and Wormuth, Pequegnat, McEachran, Hart, Cummings, Daher and Odumodii (1977).

The purpose of this study was to determine: (1) the seasonal species composition of larval fishes in Alazan Bay; (2) seasonal fluctuations in relative densities; (3) seasonal distribution of selected species; and (4) related seasonal fluctuations in temperature, salinity, and photoperiod to the larval ichthyofaunal composition and relative densities. This study was an extension of the black drum study (Project No. 8446) conducted by Mr. Steve Cornelius through Texas A&I University and funded by the Caesar Kleberg Foundation.

STUDY AREA

Alazan Bay is a hypersaline bay located within the semiarid climatic region of south Texas (27°18'N × 97°34'W) (Fig. 1). It is part of a shallow bay complex and covers approximately 5852 ha. Alazan Bay (Fig. 2) lies on a north-south line, is 24 km long and 4 km wide at its widest point (Breuer 1957).

Alazan Bay is separated from the Gulf of Mexico by Padre Island. Corpus Christi Water Exchange Pass is the nearest northern connection to the Gulf and is approximately 44 km north of the mouth of Baffin Bay. Aransas Pass is 20 km north of the Corpus Christi Water Exchange Pass. Port Mansfield Channel, which is 72 km south of the mouth of Baffin Bay, is the nearest southern connection with the Gulf of Mexico (Behrens 1966). Port Mansfield Channel and Aransas Pass are kept open and at depth continually by dredging and are the main exchange channels between the Gulf of Mexico and Laguna Madre. Corpus Christi Water Exchange Pass is not maintained and is partially closed by siltation. On 17 September 1979, storm tides produced by Hurricane Frederick breached Padre Island for approximately 3 days at Rattlesnake Pass.

In the area surrounding Alazan Bay, evaporation exceeds rainfall by 60 cm annually and, hence, the Baffin-Alazan Bay complex has been characterized by high salinities (Behrens 1966). Prior to 1949, salinities exceeding 100‰ were recorded (Collier and Hedgpeth 1950). Completion of the Intracoastal Waterway in 1949 along the length of the Laguna Madre increased water movement and reduced the probable maximum salinities in Alazan Bay to 85‰ (Behrens 1966). Freshwater inflow into Alazan Bay occurs only during periods of rain when a large portion of the surrounding watershed drains into Petronilla Creek (Fig. 2).

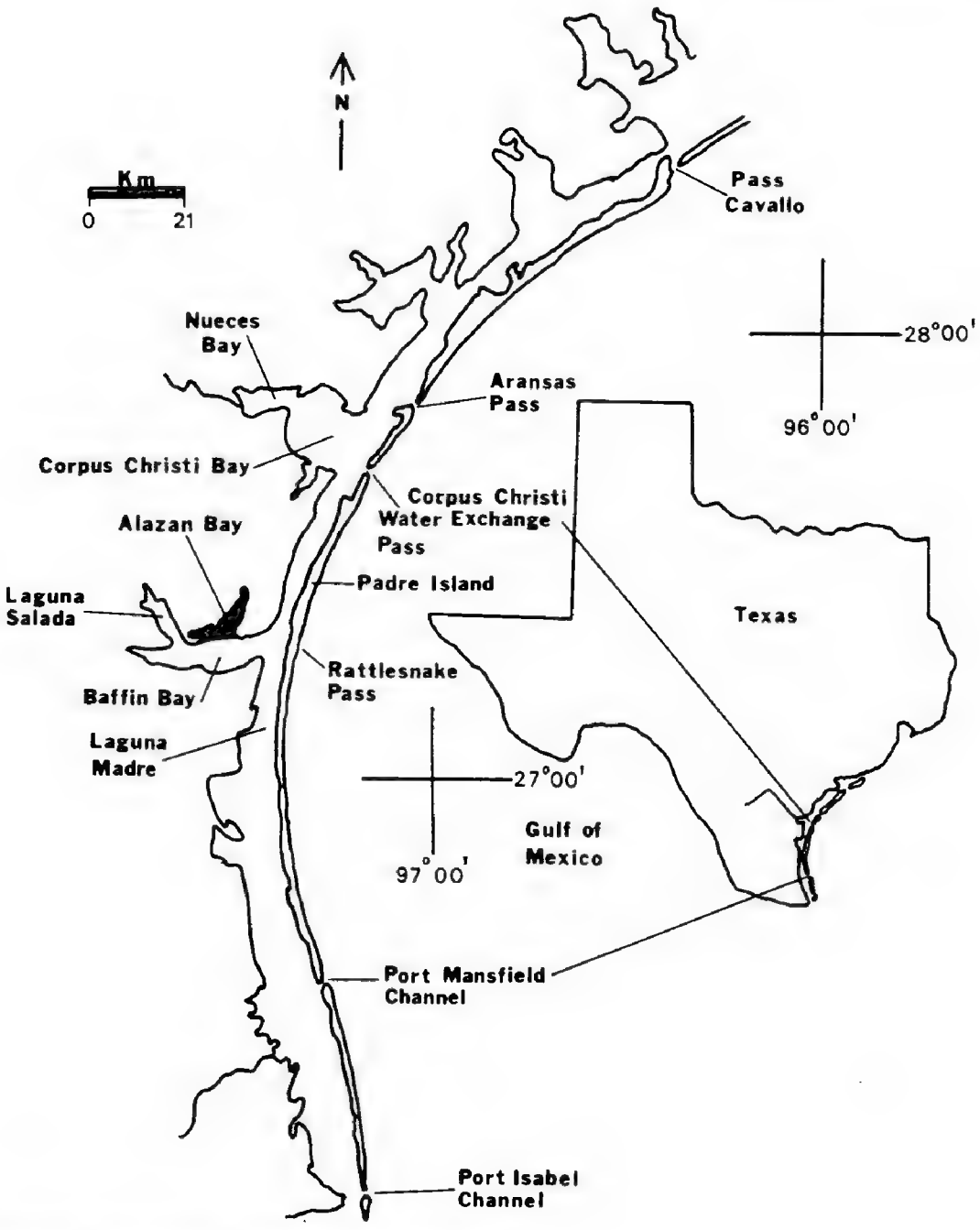

FIG. 1. Map of the south Texas coastal region.

The only notable tidal fluctuations occur during solar equinoxes in the spring and fall at which time water levels rise from 30 to 45 cm (Breuer 1957). Daily changes in the water level are primarily the result of winds (Copeland, Thompson, and Ogletree 1968). Northerly winds push the waters of Alazan Bay into Baffin Bay while southerly to southeasterly winds push the waters of Baffin Bay into Alazan Bay (Simmons 1957).

Alazan Bay has a maximum depth of approximately 2.5 m (Breuer 1957, Dalrymple 1964). Soft, black muds comprise the substrate of the central portion of the bay while bottom sediments in the shallow peripheral areas are primarily clay. Calcareous reefs formed by serpulid worms are concentrated in the mouth of Alazan Bay.

Seagrass beds of *Halodule wrightii* were present along the east shore between Starvation Point and Little Starvation Point, and beds of *Ruppia maritima* were present in the south-central portion of Cayo del Infernillo during this study (Fig. 2).

MATERIALS AND METHODS

Within the boundaries of Alazan Bay, ichthyoplankton samples were collected at five sample sites from September, 1978 through November, 1979 (Fig. 2). Each site was sampled twice

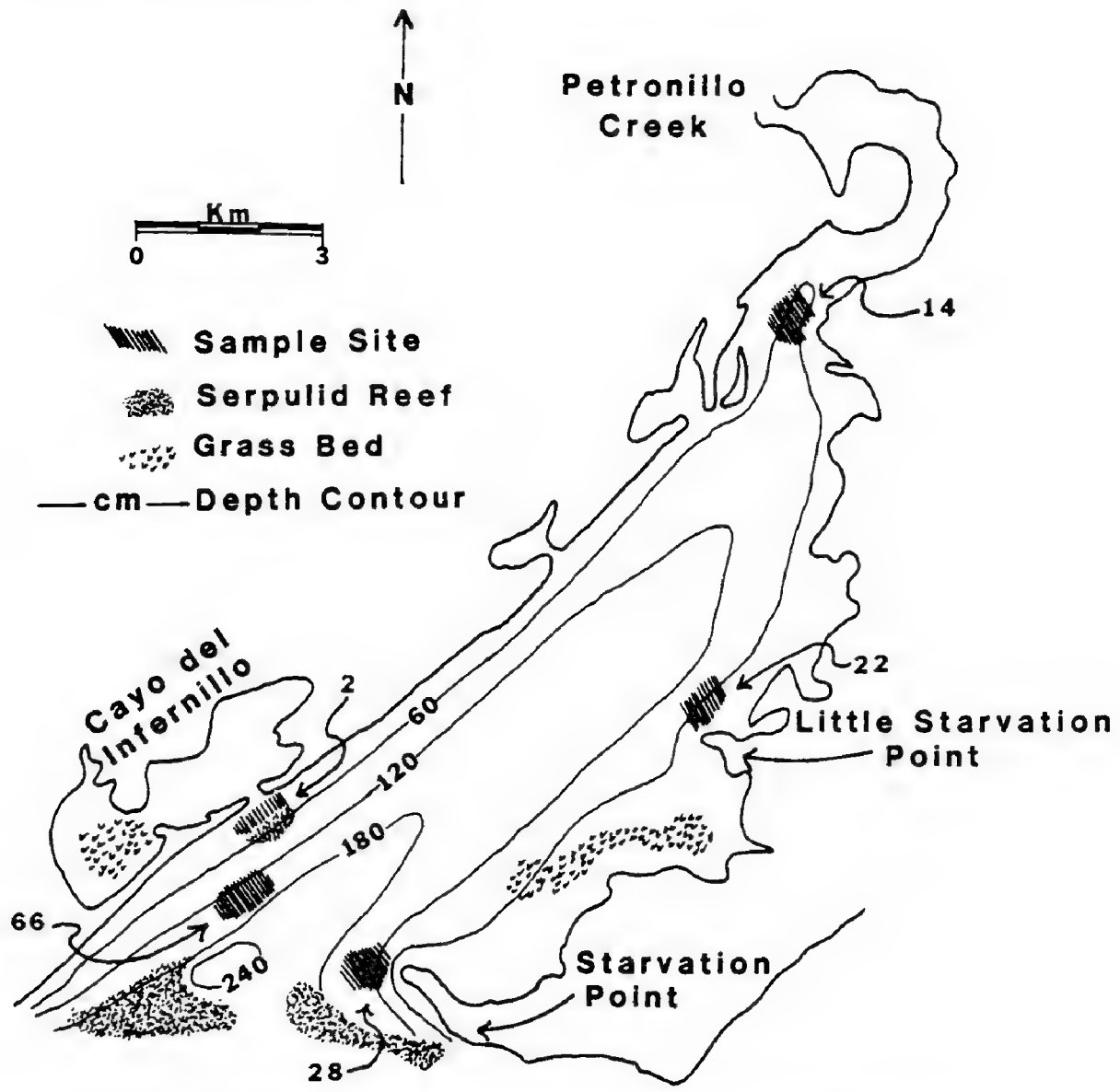

FIG. 2. Map of Alazan Bay, Texas (after Breuer 1957, Dalrymple 1964).

monthly at approximately 2-week intervals with the exceptions of September, 1978 when sample sites 2, 66, and 14 were sampled once, January and March, 1979 when all five sites were sampled once, and June, 1979 when sample site 66 was sampled once. Specimens were captured by pulling a zooplankton net (mouth dimensions of 30 cm × 80 cm, a bag length of 2.0 m, and a square mesh size of 0.7 mm) suspended from a benthic sled for 5 minutes per sample except for 5 of the 6 samples collected at Station 28 in the fall 1979 season, in which the net was pulled 3 minutes because of heavy concentrations of decaying seagrass suspended in the water column. The net was pulled by a 4.3 m long, flat-bottom boat powered by a 50-hp outboard engine except in areas too shallow where the net was pulled by hand. Each tow covered approximately the same distance.

Samples were preserved in the field in 5% borax buffered formalin (Richards and Berry 1973). Captured specimens were stained by the addition of rose bengal at the time of collection to facilitate sorting of the samples (Mitterer and Pearson 1977). After a minimum fixation period of 48 hours, the specimens were transferred to 2% formalin which had been similarly buffered. When possible each specimen collected was identified to species (Joseph, Massmann, and Norcross 1964; Dawson 1966; Lippson and Moran 1974; Fruge and Truesdale 1978; and Jones, Martin, and Hardy 1978).

Surface temperatures were measured to the nearest 1°C with a YSI Model 43 Thermistor Thermometer. Surface salinities were recorded to the nearest 1‰ at each station with a Goldberg Refractometer. Daily photoperiod was calculated from information presented by Pass (1977) by subtracting the time (CST) of sunrise from the time of sunset.

The 15-month duration of this study was arbitrarily divided into five seasons: Fall 1978 (September–November 1978), Winter 1978 (December 1978–February 1979), Spring 1979 (March–May 1979), Summer 1979 (June–August 1979), and Fall 1979 (September–November 1979). Species composition in Alazan Bay during each season was determined by dividing the number of individuals of each species caught by the total number of individuals of all species caught. A two-way analysis of variance was conducted on the mean catch per tow of all fishes combined at each station in each season (Overall and Speigel 1969). All data were transformed to common logarithms before analysis. One randomly selected data point was deleted from the fall data at each of Station 28 and 22, and one value was added to the summer data following Ott (1977) to complete the design of the analysis which specified an equal number of samples in each cell. The mean catches of *Gobiosoma* sp., *Anchoa mitchilli*, and *Microgobius thalassinus* were similarly analyzed. Duncan's New Multiple Range Test (Kramer 1956) was used to identify which mean seasonal catch rates were significantly different from the other(s) when the analysis of variance indicated significant differences.

To determine the effects of various physical parameters on seasonal abundance, a linear regression analysis of catch rate *versus* each of photoperiod, temperature, and salinity was employed for all species combined, *Gobiosoma* sp., and *A. mitchilli*.

RESULTS

Sixteen species, 6571 specimens, were collected (Table 1). Species number increased from Fall 1978 (6) and Winter 78 (4) through spring 79 (9) then decreased through Summer 79 (8) and Fall 79 (5). *Gobiosoma* sp. was the dominant species caught, and along with *Anchoa mitchilli* and *Microgobius thalassinus* accounted for > 96% of each seasonal catch and > 98% of the total catch.

Mean catch rates of larval and postlarval fishes in Alazan Bay were significantly lower in the Winter 78 (~ 2.6 fish/tow) than in the other four seasons (Fig. 3; Tables 2 and 7). There was no significant difference between Fall 78, Fall 79, Spring 79, or Summer 79 catch rates (~ 60 fish/tow). Catch rates were not significantly affected by sample site or season × site interactions.

The mean catch of larval and postlarval *Gobiosoma* sp. in Alazan Bay was significantly lower in Winter 78 (~ 2 fish/tow) than during the other four seasons (Fig. 4; Tables 3 and 7). No significant difference was determined between mean catch rates of *Gobiosoma* sp. during the Fall 78, Fall 79, Spring 79, or Summer 79 (~ 34 fish/tow). This was true of catch rates at all five stations.

Mean catch rates of larval and postlarval *Anchoa mitchilli* were significantly lower in the Fall 78, Winter 78, and Fall 79 than in the Spring 79 and Summer 79 (Fig. 5, Tables 4 and 7). Mean catches during the Fall 78, Winter 78, and Fall 79 were statistically similar (~ 2 fish/tow) as were catch rates during the Spring 79 and Summer 79 (~ 38 fish/tow). This seasonal pattern prevailed at all five stations.

Mean catch rates of larval and postlarval *Microgobius thalassinus* in Alazan Bay were significantly lower in the Fall 78 and Winter 78 (~ 0 fish/tow) than in the Summer 79 and Fall 79 seasons (~ 7 fish/tow), while the Spring 79 season (~ 1 fish/tow) was statistically consistent with all other

TABLE 1

Number of larval fishes caught during each season in Alazan Bay, Texas. (Number in parenthesis represents number of samples collected each season.)

Species	Bay				Gulf				Reference
	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	
Gobiosoma sp.		X	X	X					Springer and McErlean 1961, Hoese 1965
		X	X						Dawson 1966
			X	X					Hildebrand and Cable 1938
Anchoa mitchilli	X	X	X	X		X	X	X	Hoese 1965
				X				X	Bradley and Compton 1963
		X	X						Moseley *et al.* 1975
Microgobius thalassinus		X	X	X					Richardson and Joseph 1975
Syngnathus scovelli									
Sphoeroides parvus									
Menida beryllina		X	X	X					Gunter 1945, Renfro 1958,
									Hoese 1965
Cynoscion nebulosus		X	X	X					Pearson 1929, Miles 1950,1951
Pogonias cromis	X	X			X	X			TPWD 1975b
					X	X			Pearson 1929
	X	X							Joseph *et al.* 1964, Simmons Breuer 1962
Cyprinodon variegatus									
Micropogonias undulatus	X			X					Welsh and Breder 1923
					X			X	Pearson 1929, Bradley and Compton 1963, Hoese 1965, Compton 1965
Leiostomus xanthurus					X	X			Pearson 1929, Parker 1971
Hippocampus zosterae	X	X	X	X					Strawn 1958
Gobiesox strumosus		X		X		X		X	Hoese 1965
		X	X						Pearson 1941, Runyan 1961

seasons (Tables 5, 6, and 7). These seasonal patterns were consistent at all five stations.

Water temperatures in Alazan Bay ranged from 7°C on 12 January 1979 to 31°C on 10 July 1979 and generally declined from Fall 78 through Winter 78, increased through Spring 79 and Summer 79, and decreased through the Fall 79 (Fig. 6). The same pattern occurred at each of the five sample sites. Photoperiod, following a sine curve, ranged from 601 minutes/day in mid-December (winter solstice) to 859 minutes/day in mid-June (summer solstice). Salinities in Alazan Bay ranged from 0‰ at Station 14 on 11 and 24 September 1979 to 49‰ at Station 22 on 7 September 1978. Generally, salinities declined from Fall 78 through Fall 79 at each of the stations (Fig. 7), with less variation near the mouth of the bay (Station 28) than near the head of the bay (Station 14).

Linear regression analysis indicated that photoperiod, temperature, and salinity were all correlated with the catch of *Gobiosoma* sp., *A. mitchilli*, and all species combined (r ranged from -0.190 to 0.409) (Table 8). However, the amount of variation in the catch explained by each regression was $< 20\%$. Both temperature and photoperiod were directly correlated with fish catch while salinity was negatively correlated.

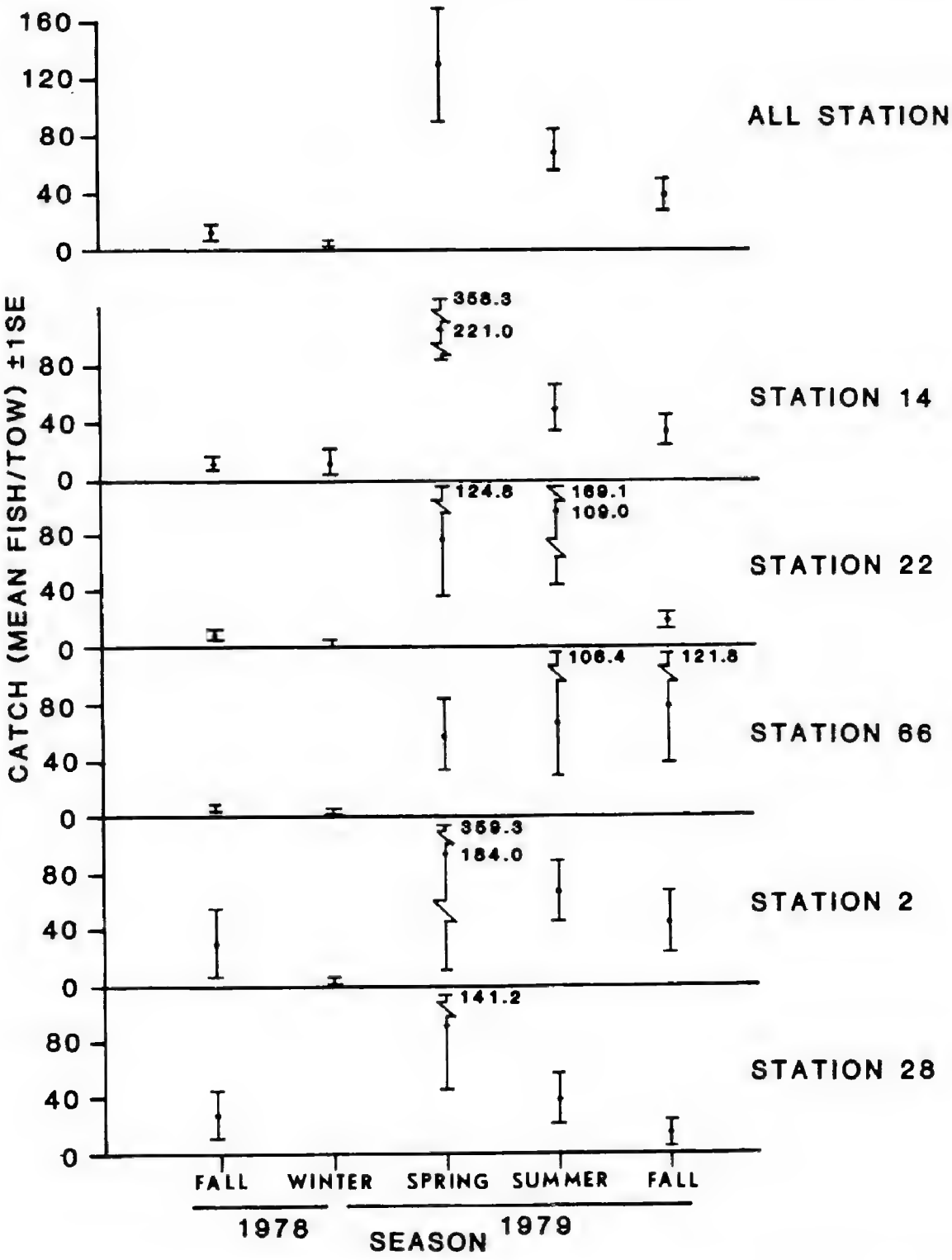

FIG. 3. Seasonal catch rates of larval fish in Alazan Bay, Texas, 1978–1979 at five sample sites.

DISCUSSION

Within Alazan Bay and the adjacent Baffin Bay complex, at least 52 species of fishes have been previously collected or observed as mature specimens (Breuer 1957, Fuls 1974, Tinnin 1974, Krull 1976). Based on the presence of larval and postlarval fishes collected, seasonal spawning patterns were evident for *Gobiosoma* sp., *Anchoa mitchilli, Microgobius thalassinus, Syngnathus scovelli, Sphoeroides parvus*, and *Menidia beryllina.* Low catches (≤ 2 specimens) of *Cynoscion nebulosus, Pogonias cromis, Cyprinodon*

TABLE 2

Results of two-way analysis of variance of mean catch (fish/tow) of all larval fish at each station in Alazan Bay during each season.

Source of variance	Degrees of freedom	Sum of squares	Mean square	*F*-Statistic
Total	135	87.211		
Seasons	4	22.141	5.535	9.955*
Stations	4	0.621	0.155	0.279 NS
Seasons X Stations	16	2.732	0.171	0.307 NS
Error	111	61.717	0.566	

* $P < 0.01$

NS = Not Significant at $P = 0.05$

variegatus, Micropogonias undulatus, Leiostomus xanthurus, Hippocampus zosterae, and *Gobiesox strumosus* preclude any conclusions on spawning patterns; however, the presence of larval and postlarval specimens of these species in Alazan Bay and the time of occurrence is generally consistent with previous reports (Table 9).

Spawning in Alazan Bay apparently occurred throughout the year by at least two species of fish, *Gobiosoma* sp. and *Anchoa mitchilli. Gobiosoma* sp. probably represented at least two gobiids, *G. bosci* and *G. robustum* (TPWD 1975a; Krull 1976; Cornelius, pers. comm., 1979).

Larval and postlarval *Gobiosoma* sp. were caught in each month except January and March while specimens of *A. mitchilli* were caught monthly except November (1978 and 1979) and March. An apparent peak in spawning occurred in May when the photoperiod was > 750 min/day, temperatures were rising (> 19°C) and the salinity was falling (< 45‰). Nelson (1928) reported that *G. bosci* began spawning when water temperatures reached 20°C and Springer and McErlean (1961) reported a temperature correlated midsummer depression in the spawning of *G. rubustum* in Tampa Bay, Florida. Larval *Gobiosoma* sp. and *A. mitchilli* may have occurred because the usually mild winters of south Texas are relatively short and involve warming trends during which shallow water temperatures approach and exceed 20°C. Hoese (1965) concluded that *A. mitchilli* could possibly be induced to spawn during brief warm periods in the cold seasons when surface temperatures reached 20°C. Dawson (1966) found no evidence of a midsummer temperature-correlated depression of spawning activity by either *G. bosci* or *G. robustum* in the more northerly waters of the Mississippi Sound. Differences in the spawning patterns of *Gobiosoma* sp. at different locations can possibly be attributed to variations in annual temperature patterns. More northern localities, Mississippi Sound, Chesapeake Bay, etc., are subject to more sharply defined seasons with longer and colder winters, without brief warming trends such as those which occur in south Texas. Arnold *et al.* (1976, 1977) reported that spawning by *Cynoscion*

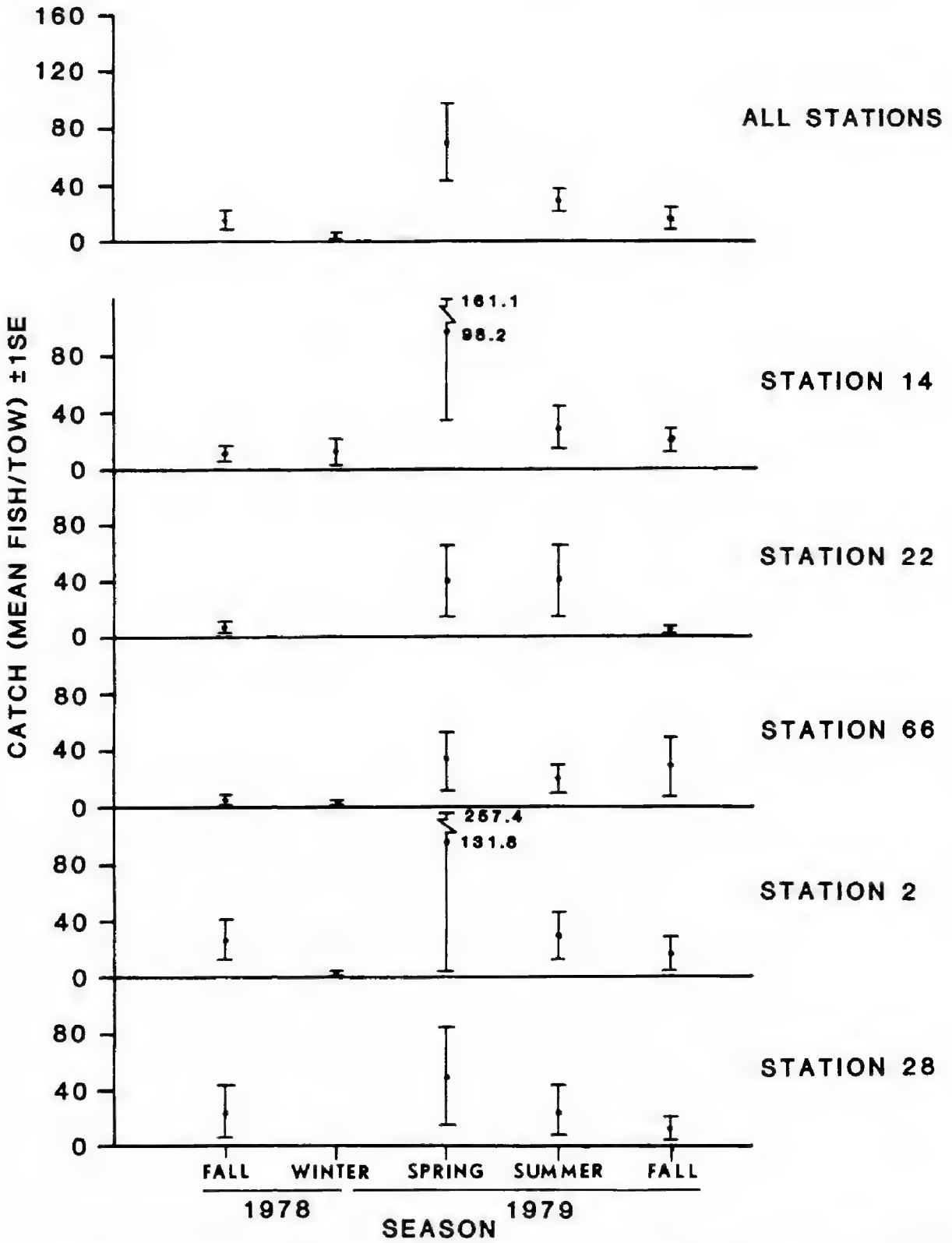

FIG. 4. Seasonal catch rates of larval *Gobiosoma* sp. in Alazan Bay, Texas, 1978–1979 at five sample sites.

nebulosus, Sciaenops ocellata, and *Paralichthys lethostigma* held in captivity could be induced by manipulating photoperiod and temperature. According to Smith (1974) temperature and light are the two most obvious stimuli in the maintenance of annual periodicity in the life cycles of plants and animals.

Linear regression analysis of salinity correlations indicate that salinity influenced spawning of *Gobiosoma* sp. in Alazan Bay to a lesser degree than either temperature or photoperiod. However, young *G. bosci* (7.5–11.0 mm) in the Mississippi Sound were most common at salinities ranging from 19.8

TABLE 3

Results of two-way analysis of variance of mean catch (fish/tow) of *Gobiosoma* sp. at each station in Alazan Bay during each season.

Source of variance	Degrees of freedom	Sum of squares	Mean square	*F*-Statistic
Total	135	74.075		
Seasons	4	14.523	3.631	7.092*
Stations	4	0.967	0.242	0.473 NS
Seasons X Stations	16	2.261	0.141	0.275 NS
Error	110	56.323	0.512	

* $P < 0.01$

NS = Not Significant at $P = 0.05$

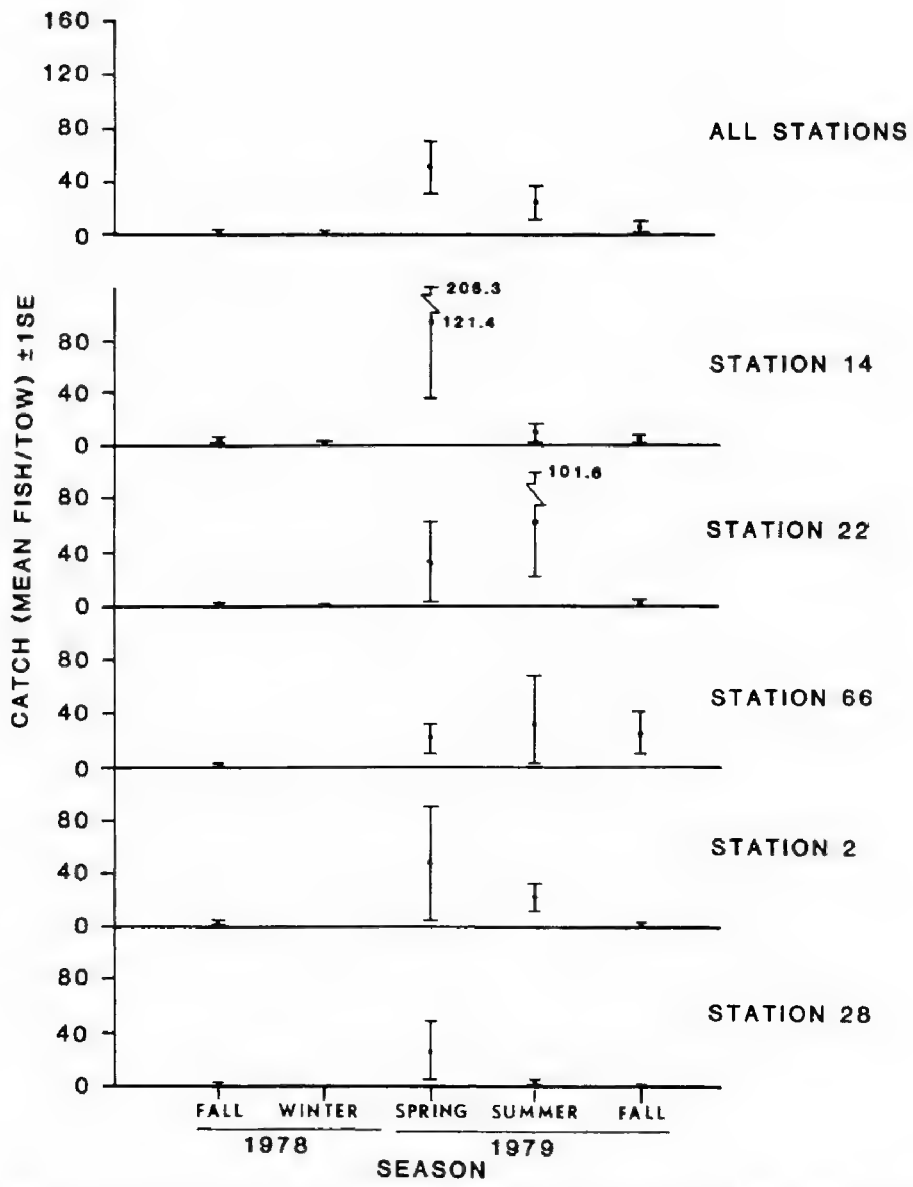

FIG. 5. Seasonal catch rates of larval *Anchoa mitchilli* in Alazan Bay, Texas, 1978–1979 at five sample sites.

TABLE 4

Results of two-way analysis of variance of mean catch (fish/tow) of *Anchoa mitchilli* at each station in Alazan Bay during each season.

Source of variance	Degrees of freedom	Sum of squares	Mean square	*F*-Statistic
Total	135	61.116		
Seasons	4	12.695	3.174	8.076*
Stations	4	0.998	0.250	0.636 NS
Seasons X Stations	16	4.167	0.260	0.662 NS
Error	110	43.256	0.393	

* $P < 0.01$

NS = Not Significant at $P = 0.05$

TABLE 5

Mean catch (fish/tow) ± 1 SE of *Microgobius thalassinus* at each station in Alazan Bay during each season.

Season	Station				
	28	2	66	22	14
Fall 78	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Winter 78	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Spring 79	0.2 ± 0.2	5.2 ± 5.0	1.2 ± 0.8	0.2 ± 0.2	1.4 ± 1.2
Summer 79	6.3 ± 4.6	8.3 ± 3.8	4.8 ± 2.0	6.3 ± 3.1	6.3 ± 5.4
Fall 79	0.0 ± 0.0	20.7 ± 11.7	15.0 ± 7.4	2.5 ± 1.8	3.5 ± 3.3

TABLE 6

Results of two-way analysis of variance of mean catch (fish/tow) of *Microgobius thalassinus* at each station in Alazan Bay during each season.

Source of variance	Degrees of freedom	Sum of squares	Mean square	*F*-Statistic
Total	135	33.490		
Seasons	4	7.409	1.852	9.851*
Stations	4	1.530	0.383	2.037 NS
Seasons X Stations	16	3.873	0.242	1.287 NS
Error	110	20.678	0.188	

* $P < 0.01$

NS = Not Significant at $P = 0.05$

TABLE 7

Results of Duncan's New Multiple Range Test for significant differences ($P = 0.05$) between the mean seasonal catch (fish/tow ± 1 SE) of all species combined, *Gobiosoma* sp., *Anchoa mitchilli*, and *Microgobius thalassinus*. Mean catch values were converted to common logarithms for analysis. Mean catch values underscored by a continuous line are not significantly different. Mean catch values underscored by different lines are significantly different.

	Season				
	Winter 78	Fall 78	Fall 79	Summer 79	Spring 79
All Species Combined	2.6 ±2.1	16.7±5.3	35.0± 11.2	64.0± 16.0	125.9± 45.0
Gobiosoma sp.	2.4 ±2.0	15.5±5.2	18.5± 5.6	30.5± 7.5	71.6± 28.1
Anchoa mitchilli	0.1 ±0.1	1.0±0.3	7.4± 3.8	26.2± 10.3	50.1± 20.2
	Winter 78	Fall 78	Spring 79	Summer 79	Fall 79
Microgobius thalassinus	0.0 ±0.0	0.0±0.0	1.6± 1.0	6.4± 1.7	8.3± 3.1

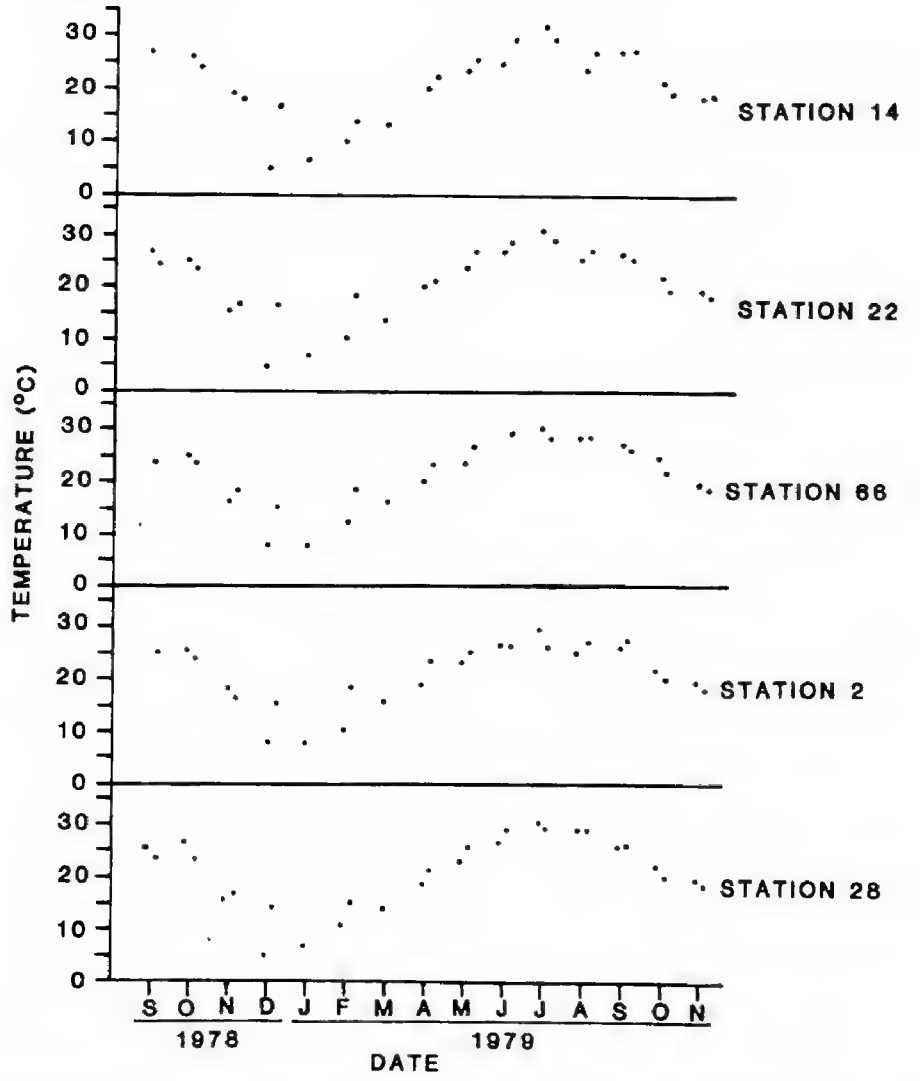

FIG. 6. Surface water temperatures at five sample sites in Alazan Bay, Texas, 1978–1979.

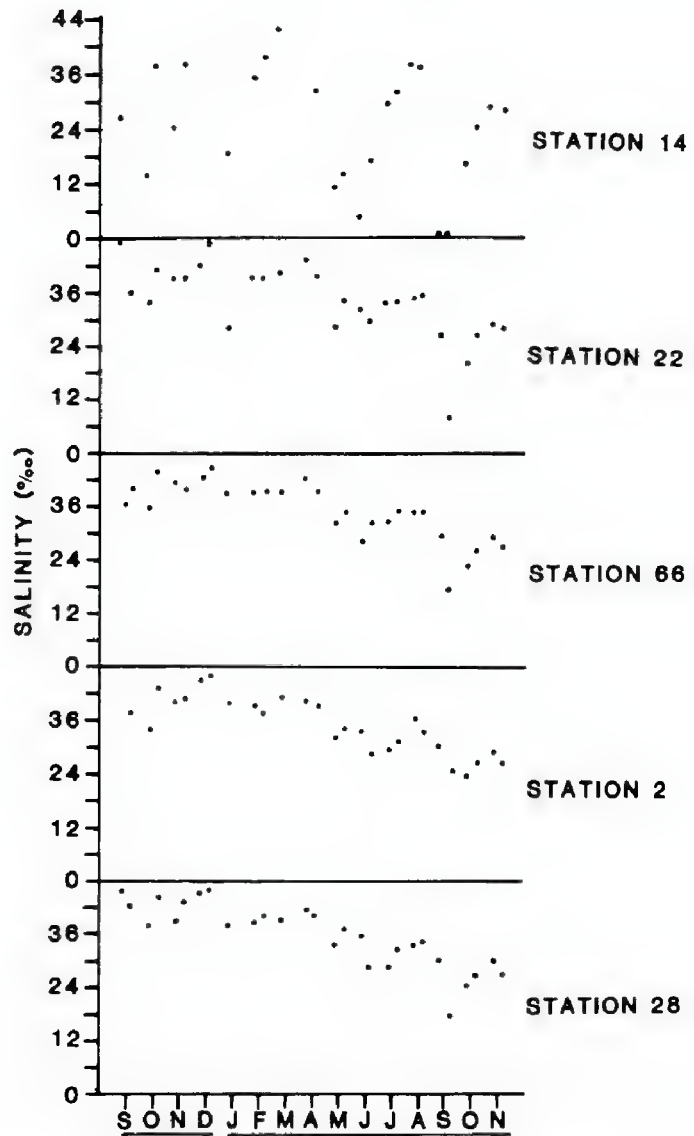

FIG. 7. Surface salinities at five sample sites in Alazan Bay, Texas, 1978–1979.

TABLE 8

Linear regression analysis of catch/tow at all stations combined as a function of temperature, salinity, and photoperiod for all species combined, *Gobiosoma* sp., and *Anchoa mitchilli*.

Variable	*N*	*r*	Slope	Intercept	r^2(100)
All species					
Temperature	136	0.250	4.56	-48.05	6.25
Salinity	136	-0.256	-3.09	150.10	6.55
Photoperiod	136	0.409	0.55	355.57	16.72
Gobiosoma sp.					
Temperature	136	0.213	2.33	-21.88	4.54
Salinity	136	-0.190	-1.38	72.89	3.61
Photoperiod	136	0.345	0.28	-181.82	12.50
Anchoa mitchilli					
Temperature	136	0.209	1.79	-20.76	4.37
Salinity	136	-0.266	1.51	66.88	7.08
Photoperiod	136	0.388	0.24	-162.65	15.05

TABLE 9

Reported spawning locations and seasons of each species represented in the ichthyoplankton samples from Alazan Bay, Texas, September 1978 through November 1979.

Species	Season					
	Fall 78 (27)	Winter 78 (25)	Spring 79 (25)	Summer 79 (29)	Fall 79 (30)	Total (136)
Gobiosoma sp.	418	60	1791	884	555	3708
Anchoa mitchilli	28	3	1285	761	222	2299
Microgobius thalassinus	1	0	41	187	250	479
Syngnathus scovelli	3	0	8	16	22	49
Sphoeroides parvus	0	0	11	0	0	11
Menida beryllina	1	0	8	1	0	10
Unidentified larvae (Bothidae)	0	0	0	4	0	4
Cynoscion nebulossus	0	0	0	2	0	2
Unidentified larvae (Gobiidae)	0	0	2	0	0	2
Pogonias cromis	0	0	1	0	0	1
Cyprinodon variegatus	0	0	0	0	1	1
Micropogonias undulatus	0	1	0	0	0	1
Leiostomus xanthurus	0	1	0	0	0	1
Hippocampus zosterae	0	0	0	1	0	1
Gobiesox strumosus	1	0	0	0	0	1
Unidentified larvae (Pleuronectiformes)	0	0	1	0	0	1
Total	452	65	3148	1856	1050	6571

to 24.7‰ (Dawson 1966). Massmann, Norcross, and Joseph (1963) reported upriver displacement of larval *G. bosci* in the York River Estuary. Data from Alazan Bay do not indicate any type of displacement of larval *Gobiosoma* sp.

All *Microgobius thalassinus* larvae collected were in the postlarval stage. Hildebrand and King (1978) reported an abundance of mature specimens of *M. thalassinus* in the seagrass beds of the upper Laguna Madre. Mature specimens of *M. thalassinus* were collected in the Baffin-Alazan Bay complex. Richardson and Joseph (1975) found *M. thalassinus* spawning from June through October in the York River estuary with some larvae found as early as March and as late as November. This spawning pattern was encountered in Alazan Bay with the exception of Fall 78. Generally, catch rates of *M. thalassinus* steadily increased from Fall 78 (0.0 ± 0.0 fish/tow) through Fall 79 (8.3 ± 3.1 fish/tow) with the difference between the two fall seasons being significant. The average water temperature for all stations during these two seasons was the same (21.9°C). However, the average salinity was higher during the Fall 78 (38.0‰) than in the Fall 79 (22.9‰). Spawning may be influenced adversely by high salinity. This conjecture is also reflected in the monthly catch rates at each station. During the month of May (Spring 79) the average salinity at Station 14 was 12.0‰ and the average catch rate of *M. thalassinus* was 90 fish/tow while the average salinity at

each of the other four sample stations was > 31.0‰ and the average catch rate was ~ 13 fish/tow.

Syngnathus scovelli is a common pipefish in the grass beds of the Laguna Madre (Hildebrand and King 1978). Of all *S. scovelli* collected, > 75% were captured at Stations 28 and 22, both of which are in relatively close proximity to the *Halodule wrightii* grass beds in the shallow waters along the east shore of Alazan Bay during the Summer 79 and Fall 79 seasons.

Sphoeroides parvus was collected only during the month of April in the Spring 79, which indicated a limited spawning season. Mature specimens were common in Baffin Bay. The fact that the larvae were collected only near the mouth of Alazan Bay at Stations 28 and 66 indicated that spawning occurred in Baffin Bay and the young were transported into Alazan Bay.

Hellier (1962) reported mature specimens of *Menidia beryllina* in spawning condition to be common in the upper Laguna Madre, and Hildebrand and King (1978) found adult populations of *M. beryllina* to be abundant in the shore zone of the upper Laguna Madre. Krull (1976) found this also to be true within the Laguna Salada. Gunter (1945), Renfro (1958), and Hoese (1965) reported *M. beryllina* to have a bimodal spawning pattern with peaks in the spring and fall. In Alazan Bay larval specimens were collected in Fall 78, Spring 79, and Winter 79 but not in sufficient numbers to draw any conclusions regarding bimodal spawning schemes.

The data collected during this study suggest that, although Alazan Bay is not a major spawning site or nursery for commercially important finfish of the Texas coast, it is extensively utilized as a spawning site by fishes which provide a key link in the food chain of commercially important fishes as well as various water birds and other non-commercial fishes (Dawson 1966, Hildebrand 1963).

ACKNOWLEDGMENT

Drs. Bart Cook and Wes Tunnell (Dept. of Biology, Corpus Christi State University) and Kay Dokken (Corpus Christi, Texas) all deserve special thanks for their contributions to this study.

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